THE ECOLOGY OF THE CAPE GRASS LIZARD, *CHAMAESAURA ANGUINA*

by

Annemarie du Toit

Department of Zoology, University of Stellenbosch

Thesis presented in partial fulfilment of the requirements for the degree Master of Science at the University of Stellenbosch

Supervisor: Prof. P. le F.N. Mouton

Co-supervisor: Dr. A.F. Flemming

March 2001

Declaration

I the undersigned hereby declare that the work contained in this thesis is my own original work and has not previously in its entirety or in part been submitted at any university for a degree.

CONTENTS

CHAPTER 2. TEMPERATURE PREFERENCE, MOVEMENT PATTERNS AND MICROHABITAT USE IN THE CAPE GRASS LIZARD, *CHAMAESAURA ANGUINA*

CHAPTER 3. REFUGE SELECTION AND SUSCEPTIBILITY TO FIRE IN THE CAPE GRASS LIZARD, *CHAMAESAURA ANGUINA*

ABSTRACT

The foraging mode of the Cape grass lizard, *Chamaesaura anguina*, was determined by using three criteria: 1) the number of movements per minute (MPM) and the percentage of time spent moving (PTM) during periods of activity; 2) the amount of tongue-flicking directed at cotton applicators labelled with prey chemicals as a measure of prey chemical discrimination; 3) the stomach contents of the lizards as an indication of the natural diet. Observations were made by means of binoculars from an observation tower using a seminatural outdoor enclosure, and through a one-way glass panel using a seminatural indoor enclosure. Each lizard was observed for a 10 minute period during peak activity and the times it was moving and the times it was stationary were recorded. Data obtained in the indoor- and outdoor enclosures did not differ significantly and were pooled. MPM (0.37 ± 0.21 SD) and PTM (1.92 % ± 0.93 SD) values recorded for *C. anguina* (N = 10) fall within the range given as characteristic for sit-and-wait foragers. Nine *C. anguina* individuals were habituated in glass terraria to accept mealworms offered to them. When all lizards accepted food without hesitation, they were tested for their ability to discriminate among three different odours presented to them in a randomized block design: prey odours consisting of mealworm surface odours, distilled water as an odourless control stimulus, and cologne as a pungency control. The number of tongue-flicks directed at the cotton applicator containing the stimulus odour during 60 s was recorded. No statistically significant differences were found among the responses to the three treatment odours (Kruskal-Wallis, H = 2.41, *df* = 2, P = 0.30). An analysis of the stomach contents of 21 *C. anguina* specimens revealed a diet of mostly diurnally active arthropod prey species.

The preferred body temperatures selected by 12 grass lizards in a thermal gradient were measured six times during a 48 hour period, using a copper-constantan thermocouple inserted into the cloaca. The measured body temperatures (N = 72) ranged from 22.62 °C - 27.07 °C with a mean of 24.82 °C ± 2.27 SD. The low preferred body temperature exhibited by *C. anguina* as compared to other cordylids may be attributed to the combined influence of vegetative cover, high altitude, and high surface-volume ratio. To determine movement patterns and microhabitat use, six lizards were observed in a seminatural outdoor enclosure (4 x 4 m). The location of the grass tufts in the enclosure was mapped, and the position of each lizard within the enclosure was noted on 17 mornings. Observations of lizard behaviour during periods of activity were made by means of binoculars from an observation tower. Although *C. anguina* did not show reliance on a specific shelter site, the taller, broader tufts were generally preferred as refuges during inactivity. There were significant differences between the heights (student's *t*-test; $P < 0.001$) and the diameters (Mann-Whitney; $P < 0.001$) of the preferred grass tufts, and those grass tufts that were not preferred as refuges, respectively. The lizards usually sheltered in a coiled-up position in the middle of the grass tufts close to the ground. During active periods, the lizards perched in an elevated position in the vegetation by entangling their elongated bodies and tails in the grass for efficient weight distribution. Locomotion was mainly restricted to the strike action when attacking prey.

Fynbos and grassland, which are the main habitat of grass lizards of the genus *Chamaesaura*, are fire-prone. With their serpentiform morphology, grass lizards differ markedly from other cordylids, the majority of which are rock-dwelling. One aim of this study was to determine whether grass lizards make use of refuges like burrows or crevices within their grass/restioid habitat during periods of inactivity or when

threatened by fire. Refuge selection during inactivity was determined experimentally. Twelve lizards were offered different refuge options, namely grass tufts, crevices, burrows and loose sand. All twelve lizards preferred to shelter in the grass tufts. When the grass tufts were removed, only two lizards made use of the burrows and crevices provided, the other 10 not sheltering at all. Refuge selection when threatened by fire was tested by placing the 12 lizards in an enclosure provided with grass tufts and two types of refuges, burrows and crevices. The grass was set alight at one end of the enclosure and the fire was fanned on towards the other end with the aid of a high-speed fan. Precautions were taken to ensure the safety of all the lizards and to intervene when they were in direct danger. Only two of the 12 lizards sought shelter in the refuges provided. Of the remaining 10, six fled and four were trapped by the flames, requiring intervention. The results of these experiments, as well as field observations, suggest that *C. anguina* seldom makes use of shelter options other than grass and restio tufts, even when threatened by fire. In the case of fire, it flees by 'grass-swimming'. Field observations also suggest that mortality during and after a fire is considerably higher than in the case of rock-dwelling cordylids.

The reproductive status of adult females (N = 85) were determined on the basis of the developmental stage of ovarian follicles and the presence or absence of oviductal eggs. Females were grouped into four reproductive categories: pre-vitellogenic, early vitellogenic, pre-ovulatory and gravid. To determine the reproductive cycle exhibited by the males (N = 46), testicular volume and seminiferous tube diameter were measured, as well as the spermatogenic activity assessed qualitatively. Spermatogenic activity was assessed by using Licht's (1967) classification system. The snout-vent length (SVL) of 144 specimens was measured. Sexual size dimorphism (SSD) recorded for *C. anguina* was quantified by a size dimorphism index (SDI). Reproductive activity

was asynchronous among females, differing from the normal cordylid cycle of autumn/winter vitellogenic activity, followed by winter/spring ovulation and gestation in late summer to autumn. The significant seasonal variation that existed in testes volume (ANOVA; $F_{(7,22)} = 3.70$; $P < 0.05$) and seminiferous tubule diameter (ANOVA; $F_{(10,25)} = 4.90$; $P < 0.05$), as well as sermatogenic activity as observed by histological examination, indicated that *C. anguina* males follow an annual spermatogenic cycle that can be described as post-nuptial. The cycle is characterized by summer/autumn spermiogenesis, associated with sperm storage throughout winter. *Chamaesaura anguina* males differ from other cordylids following a post-nuptial cycle, by starting with spermatogenesis in spring. The mean SVL of female grass lizards (109.51 mm ± 20.60 SD) was significantly larger (Mann-Whitney; $P < 0.001$) than that of males (84.77 mm ± 9.39 SD). A positive SDI of 1.29 and a SDImax of 1.40 were determined. Female-biased dimorphism in SVL recorded for *C. anguina* corresponds with the general pattern recorded for terrestrial cordylids, but contrasts with male-biased dimorphism in rupicolous forms. The longer SVL of *C. anguina* females facilitates higher fecundity. This, in turn, might be an adaptive survival strategy for this lizard species in the fire-prone environment where it occurs, because successful recruitment is facilitated by high fecundity.

KEYWORDS: *Chamaesaura anguina*; serpentiform body; cryptic colouration; grass/restio habitats; undulatory locomotion; foraging mode; preferred body temperature; movement patterns; microhabitat use; fire susceptibility; refuge selection; reproductive cycle; sexual size dimorphism.

UITTREKSEL

Die voedingswyse van *Chamaesaura anguina* is bepaal deur drie kriteria: 1) die getal bewegings per minuut (BPM) en die persentasie tyd wat aan beweging bestee word (PTB) tydens aktiewe periodes; 2) die hoeveelheid tongskiete wat gerig word na watteplUisies bedek met prooi chemikalieë as 'n maatstaf van prooi chemiese diskriminasie; 3) die maaginhoud van die akkedisse as 'n indikasie van hul natuurlike diëet. Waarnemings is met 'n verkyker vanaf 'n waarnemingstoring langs 'n buitemuurse kampie gemaak, terwyl dit deur 'n eenrigting glaspaneel in die geval van 'n binnemuurse opstelling gemaak is. Elke akkedis is vir 'n periode van 10 minute tydens piek-aktiwiteit dopgehou, en die tye wat dit beweeg het en nie beweeg het nie, is aangeteken. Data verkry in die binnemuurse - en buitemuurse opstellings het nie statisties van mekaar verskil nie en is saamgevoeg. BPM (0.37 ± 0.21 SD) en PTB (1.92 % ± 0.93 SD) waardes aangeteken vir *C. anguina* (N = 10) val binne die reeks waardes wat as kenmerkend vir sit-en-wag voeders beskou word. Nege *C. anguina* individue is in glas terraria gewoond gemaak om meelwurms te aanvaar wat hul aangebied is. Toe al die akkedisse die kos sonder huiwering aanvaar het, is hul vermoë getoets om tussen drie verskillende geure wat hul aangebied is in 'n ewekansige blokontwerp, te diskrimineer: prooigeur bestaande uit die reuk van meelwurms, gedistilleerde water as 'n geurlose kontrole stimulus, en reukwater as 'n skerp kontrole. Die hoeveelheid tongskiete gerig na die gegeurde watteplUisie gedurende 'n 60 s periode, is aangeteken. Geen statisties-beduidende verskille is gevind tussen die reaksies tot die drie geure nie (Kruskal-Wallis, H = 2.41, *df* = 2, P = 0.30). 'n Analise van die maaginhoude van 21 *C. anguina* individue het meestal dag-aktiewe arthropoda prooispesies onthul.

Die voorkeur liggaamstemperature wat deur 12 akkedisse in 'n termiese gradiënt geselekteer is, is ses maal gemeet gedurende 'n 48 uur periode, deur van 'n termo-koppel wat in die kloaka geplaas is, gebruik te maak. Die bepaalde liggaamstemperature (N = 72) het gevariëer van 22.62 °C - 27.07 °C met 'n gemiddeld van 24.82 °C ± 2.27 SA. Die lae voorkeur liggaamstemperatuur van *C. anguina* mag dalk toegeskryf word aan die gekombineerde invloed van plantbedekkingskadu, hoë hoogte bo seevlak, en hoë oppervlakte-volume verhouding. Die bewegingspatrone en mikrohabitat-gebruik van *C. anguina* is bestudeer deur ses akkedisse in 'n buitemuurse kampie aan te hou. Die ligging van die graspolle binne die kampie is op 'n kaart aangeteken, en die posisie van elke akkedis binne in die kampie is op 17 oggende aangeteken. Verdere waarnemings is gemaak met 'n verkyker vanaf 'n waarnemingstoring terwyl die akkedisse aktief was. Alhoewel die *C. anguina* individue nie herhaaldelik 'n spesifieke skuilplek gebruik het nie, het hul die langer, breër graspolle as skuilplek gedurende onaktiwiteit verkies. Daar was 'n hoogs beduidende verskil tussen onderskeidelik die hoogtes (studente *t*-toets; $P < 0.001$) en die deursnitte (studente *t*-toets; $P < 0.001$) van die verkose graspolle, en die graspolle wat nie gekies is as skuilplekke nie. Hulle het gewoonlik in 'n opgerolde wyse, in die middel en na aan die bodem van die graspolle, geskuil. Daar is gevind dat *C. anguina* vanaf 'n verhewe posisie voed deur sy verlengde liggaam en stert in die grass te vervleg om doeltreffende gewigsverspreiding te verseker. Beweging was hoofsaaklik tot die vangaksie van prooi beperk.

Vuur is 'n algemene verskynsel in fynbos en graslande, wat die hoof habitat van grasakkedisse van die genus *Chamaesaura* uitmaak . Met hulle slangagtige morfologie, verskil grasakkedisse drasties van ander lede van die Cordylidae, waarvan meeste rotsbewonend is. Die doelwit van hierdie studie was om te bepaal of die grasakkedisse gebruik sal maak van skuilplekke, soos gate en klipskeure binne die grashabitat,

gedurende periodes van onaktiwiteit of wanneer bedreig word deur vuur. Twaalf akkedisse is verskillende skuilopsies aangebied, naamlik graspolle, klipskeure, gate en los sand. Al twaalf het verkies om in die graspolle te skuil. Toe die graspolle verwyder is, het slegs twee akkdisse die klipskeure en die gate benut, terwyl die ander 10 nie geskuil het nie. Skuilplek-seleksie wanneer bedreig word deur vuur, is getoets deur 12 akkedisse in 'n afskorting te plaas wat met graspolle en twee tipes skuilplekke, gate en klipskeure, voorsien is. Die gras aan die een kant van die afskorting is aan die brand gesteek en is aangehelp m.b.v. 'n hoë-spoed waaier. Voorsorgmaatreëls om die veiligheid van al die akkedisse te verseker en om in te gryp as hulle in direkte gevaar sou verkeer, is getref. In twee van die 12 gevalle het die akkedisse skuiling gesoek in die beskikbare skuilings. In die oorblywende 10 gevalle het ses akkedisse gevlug, terwyl vier deur die vlamme vasgevang was en daar ingegryp moes word. Die resultate van hierdie eksperimente, sowel as waarnemings wat in die veld gemaak is, dui daarop dat *C. anguina* selde van skuilopsies, anders as graspolle en restio's, gebruik maak as hulle deur vuur bedreig word. In die geval van vuur, vlug hulle deur te "swem" deur die gras. Veldwaarnemings dui ook daarop dat mortaliteit gedurende en na die vuur heelwat hoër is as in die geval van rotsbewonende gordelakkedisse.

Die reproduktiewe status van volwasse wyfies (N = 85) is bepaal deur die ontwikkelingsfase van ovarium follikels te ondersoek en deur die teenwoordigheid of afwesigheid van eiers in die oviduk. Wyfies is in vier reproduktiewe kategorieë gegroepeer: pre-vitellogenies, vroeg vitellogenies, pre-ovulatories en dragtig. Testikulêre volume en saadbuisdeursnit is gemeet, en spermatogeniese aktiwiteite soos histologies vasgestel, is gebruik om die reproduktiewe siklus van die mannetjies (N = 46) te bepaal. Spermatogeniese aktiwiteit is bepaal deur van Licht (1976) se klassifikasie sisteem gebruik te maak. Die snoet-kloaak lengte (SKL) van 144 individue

is gemeet en die seksuele grootte-dimorfisme (SGD) soos bepaal vir *C. anguina*, is gekwantifiseer deur middel van 'n grootte-dimorfisme-indeks (GDI). Voortplantingsaktiwiteit in die wyfies was nie gesinchroniseerd nie, en verskil dus van die normale gordelakkedissiklus met herfs/winter vitellogeniese aktiwiteit, winter/lente ovulasie en swangerskap in die volgende laat somer tot herfs. Die beduidende seisoenale verskil wat bestaan het in die testesvolume (ANOVA; $F_{(7.22)} = 3.70$; $P < 0.05$) en die saadbuisdeursnit (ANOVA; $F(10,25) = 4.90$; $P < 0.05$), asook testis histologie, het aangedui dat *C. anguina* mannetjies 'n jaarlikse spermatogeniese siklus volg, beskryf as "post-nuptial". Hierdie siklus word gekenmerk deur somer/herfs spermiogenese, geassosieer met spermstoring gedurende die winter. In teenstelling met ander gordelakkedisse wat hierdie siklus volg, begin spermatogenese in *C. anguina* alreeds in die lente. Die gemiddelde SVL van die wyfies (109.51 mm ± 20.60 SA) was beduidend groter (Mann-Whitney; $P < 0.001$) as dié van die mannetjies (84.77 mm ± 9.39 SA). 'n Positiewe GDI van 1.29 en 'n GDImax van 1.40 is gemeet. Wyfie-plus dimorfisme in SKL bepaal vir *C. anguina*, stem ooreen met die algemene patroon waargeneem by terrestriële gordelakkedisse, maar is in kontras met mannetjie-plus dimorfisme by rotsbewonende vorme. Die langer SKL by wyfies van *C. anguina* kan 'n hoër fekunditeit fasiliteer. Dit mag dalk 'n oorlewingstrategie vir die species wees wat in 'n vuurgeteisterde omgewing voorkom, omdat suksesvolle rekolonisering deur 'n hoë fekunditeit aangehelp word.

TREFWOORDE: *Chamaesaura anguina*; slangagtige liggaam; kriptiese kleuring; gras/restio habitatte; kronkel beweging; voedingsmetode; voorkeurtemperatuur; bewegingspatrone; mikrohabitat-gebruik; vatbaarheid vir vuur; skuilplekseleksie; voortplantingsiklus; seksuele dimorfisme.

ACKNOWLEDGEMENTS

I wish to thank the following people and institutions for assistance during this study:

My study leader, Prof. P. le F.N. Mouton, for his guidance, enthusiasm, and personal interest in my study, as well as for assistance with fieldwork.

Dr. A.F. Flemming, my co-study leader, for his contribution to the success of this study, for assistance with fieldwork, for his help in the statistical analyses of the data, and for his support and constructive discussions.

The Foundation for Research Development and the University of Stellenbosch, for financial support which made this study possible.

Dr. H. Geertsema, from the Department of Entomology of the University of Stellenbosch, for his valuable assistance in classifying the prey items in the stomach contents.

Cara Nieuwoudt, Louise Visagie, Niel Retief, Dahné du Toit, Antoinette du Toit, Pierre du Toit and Yolandé Mouton who provided valuable assistance with fieldwork and experiments.

Mr. A.J.J. Kotzé for permission to use his property for the execution of the fire experiments.

The Botany Department of the University of Stellenbosch for permission to use the Duthie Reserve for the construction of the outdoor enclosure.

Oscar Master Builders for providing the scaffolding and building material.

The S.A. Museum, the P.E. Museum, the Transvaal Museum and the Zoology Department of the University of Stellenbosch for specimens.

Mr. N. Papadakis of Joostenberg, Mr. G. de Jager of Du Toitskloof Pass, Mr. F. du Plessis of Jonaskop and Mr. B.P. Burger of Montagu for permission to collect specimens on their farms.

The CSRI and Agrimed for providing weather data.

Mr. L. Lourens of the Hottentots Holland Nature Reserve, Mr. M. Scott of the Swartberg Nature Reserve, Mr. M. Johns of the Kogelberg Nature Reserve, Mr. P.J. du Toit of the Cape Point National Park and Mr. J. van Deventer of the Groot Winterhoek Wilderness Area for permission to collect specimens and for offering accommodation.

Mr. M. Gentle and Dr. E. Baard of the Cape Nature Conservation Board for helpful information and assistance with fieldwork.

J.D. Kotzé for his fieldwork- and technical assistance. His patience, support, encouragement and constructive input is greatly appreciated.

Mrs. S. Wessels for her assistance in editing the manuscript.

My parents for their assistance, interest and motivation throughout this study.

GENERAL INTRODUCTION

The Cordylidae, a family of scincomorph lizards restricted to the African continent, comprises two subfamilies (Cordylinae and Chamaesaurinae) and four genera (*Cordylus*, *Pseudocordylus*, *Platysaurus* and *Chamaesaura*) (Branch 1998). The family includes rupicolous, terrestrial and grass-living forms, and preliminary species-level cladistic analyses showed that terrestrial and grass-living lifestyles represent derived conditions, a rupicolous lifestyle being the primitive one (Mouton & Van Wyk 1997; Frost *et al.* 2000).

In contrast to the mainly rupicolous genera, *Cordylus*, *Pseudocordylus* and *Platysaurus* (subfamily Cordylinae) that have normally proportioned bodies and limbs (stocky bodies, well-developed limbs), the grass lizards of the genus *Chamaesaura* (subfamily Chamaesaurinae) exhibit extreme body elongation (tail 3 - 4 times longer than SVL) and greatly reduced limbs. The phenomenon of body elongation is a common evolutionary trait in reptiles, seen in amphisbaenians, snakes, and various lizard lineages including skinks, gerrhosaurids, anniellids, anguids and cordylids (Gans 1986). Gans (1975) suggested that possible selective advantages for the evolution of body elongation and limblessness included more efficient locomotion, the ability to use crevices, the ability to burrow in soil, and the ability to use a more successful reproductive strategy, like higher fecundity. Although the generic name of the grass lizards translates more accurately as 'creeping lizards' (Branch 1998), they move, or rather 'swim' through the grass with great speed and agility. All three species of this genus occur in escarpment and montane grasslands in southern Africa, with *Chamaesaura aenea* confined to the eastern districts of South Africa, *Chamaesaura macrolepis* also occurring in the eastern regions of South Africa, but with an isolated

population on the Chimanimani Mountains of Zimbabwe, and *Chamaesaura anguina* (Figure A) occurring in grass or fynbos habitats, along the southern and eastern coastal regions of South Africa, with remote populations in Angola and in the grasslands of eastern Zaire and East Africa (Lang 1991; Mouton & Van Wyk 1997; Branch 1998). Ecological information on the genus *Chamaesaura* is limited. In this study, the ecology of *C. anguina* was studied as representative of the elongated forms in the genus. Features of the anatomy, behaviour, foraging tactics, diet, refuge selection, thermoregulation and reproductive biology of *C. anguina*, reported on in this study, can be interpreted as coadapted phenotypic traits, complementing one another to make this lizard ecologically successful.

This thesis includes four chapters, each prepared as a separate article. Repetition, especially in the introductory paragraphs, was therefore unavoidable.

THE AIMS OF THIS STUDY

I. *To determine the foraging mode followed by Chamaesaura anguina. Cordylus*, *Pseudocordylus* and *Platysaurus* are all classified as sit-and-wait foragers, while no information is available for *Chamaesaura*. Based on the conservativeness of foraging mode, one would expect members of this genus to be sit-and-wait foragers as well. The question that arises, however, is whether sit-and-wait foraging in a grass habitat will require such pronounced body-elongation as observed in *Chamaesaura*. The three main criteria used to infer foraging mode were: (1) the number and duration of movements related to foraging, quantified as the MPM (number of movements per minute) and PTM (the percentage of time spent moving); (2) the amount of tongue-flicks directed at different odours

Figure A. The Cape grass lizard, *Chamaesaura anguina*, occurring in grass/restio habitats, along the southern and eastern coastal regions of South Africa.

as a measure of prey chemical discrimination; and (3) the stomach contents of individuals as an indication of its natural diet.

II. *To conclude the preferred body temperatures of C. anguina, and to report on the movement patterns and microhabitat use exhibited by this species.*

III. *To determine whether C. anguina would make use of refuges such as burrows or crevices within its grass habitat during inactivity or when threatened by fire, which is a frequent hazard in the fynbos and grass habitats.* Laboratory experiments and field data were used to determine refuge selection and susceptibility to fire in this species.

IV. *To study reproduction in C. anguina, with the objectives to document the reproductive cycles for both males and females, as well as to determine whether sexual dimorphism occurs in this species.* The Cordylidae comprises three viviparous genera namely *Cordylus*, *Pseudocordylus* and *Chamaesaura*, and one oviparous one, *Platysaurus*. Bearing in mind the susceptibility to fire of this species, one would expect certain adaptations, regarding timing of reproductive events and fecundity, to facilitate successful recruitment after a fire. Information regarding size sexual dimorphism (SSD) in female lizards can be used as indication of fecundity. No studies examining reproductive cyclicity or sexual dimorphism in *Chamaesaura* have been done to date.

CHAPTER ONE

FORAGING MODE IN THE CAPE GRASS LIZARD, *CHAMAESAURA ANGUINA*

1.1 INTRODUCTION

The specific behaviour of predators which ensures the success of the search for prey is known as foraging strategy (Avery *et al.* 1987). Foraging strategies are known to be phylogenetically conservative within lizard families (Wapstra & Swain 1996). Lizards have traditionally been divided into active foragers and sit-and-wait predators (MacArthur & Pianka 1966; Pianka 1966; Huey & Pianka 1981), but as pointed out by MacLaughlin (1989), Garland (1993), Garland & Losos (1994) and Perry (1999), the two divisions represent extremes of a continuum, rather than an actual dichotomy. Active foraging consists of searching for prey during locomotion and/or requiring frequent locomotion and other active searching actions such as digging (Cooper 1994a). Sit-and-wait foraging, on the other hand, is defined in the traditional sense of low frequency of movement and high percentage of capture attempts initiated from a standstill (Cooper 1994a). Foraging mode is determined empirically by measuring two variables, namely the number of movements made per minute (MPM) and the percentage of time spent moving (PTM), following Cooper *et al.* (1997). Although the dividing line between the actively foraging and sit-and-wait foraging strategies is determined arbitrarily, there is a clustering of species at the extremes (Pianka 1973) which makes categorization in most cases fairly easy.

It appears that foraging mode influences numerous aspects of the lives of lizards, including reproduction (Huey & Pianka 1981; Vitt & Price 1982), anti-predator behaviour (Vitt 1983), and chemosensory behaviour (Cooper 1995). In lizards, prey

chemical discrimination, mediated by tongue-flicking, is highly correlated with foraging mode (Cooper 1989, 1990a, b, 1992, 1994a, b, 1995, 1997; Cooper & Van Wyk 1994). The tongue gathers chemicals for transfer to the vomeronasal organ, thereby sampling the environment for cues indicating the presence of prey (Halpern & Kubie 1980; Cooper & Burghardt 1990; Cooper & Van Wyk 1994). Active foragers tongue-flick at higher rates while foraging than sit-and-wait foragers, and rely more on chemical senses in locating and/or discriminating between prey and non-prey items (Bissinger & Simon 1979; Huey & Pianka 1981; Cooper 1989, 1995; Cooper & Van Wyk 1994). In general, sit-and-wait foragers rarely tongue-flick, and rather rush at visually detected prey and bite without preliminary chemosensory testing (Bissinger & Simon 1979; Cooper 1989, 1992, 1995, 1997). Stationed on some sort of perch, sit-and-wait foragers remain in one location for some time, thus conveniently benefiting from the advantages of crypsis and immobility which can be viewed as their primary defense mechanisms (Bissinger & Simon 1979; Vitt & Price 1982; Stamps 1983).

The Cordylidae is a small family of lizards endemic to Africa. It is partitioned into two subfamilies and four genera. Three of the four genera, namely *Cordylus*, *Pseudocordylus* and *Platysaurus*, are classified as sit-and-wait foragers (Cooper *et al.* 1997; Mouton *et al.* 1999). No information is available for the genus *Chamaesaura*, but based on the conservativeness of foraging mode, one would expect members of this genus to be sit-and-wait foragers as well. The three species in this genus, however, differ markedly from other cordylids in morphology in that they all have elongate, snake-like bodies, with minute fore- and hind limbs (Branch 1998). Unlike most other cordylids, which are rock-dwelling, *Chamaesaura* species are grass-living and occur in grass and restio habitats (Branch 1998). It is generally assumed that their snake-like bodies and reduced limbs are adaptations to facilitate movement in the dense vegetation

where they occur (Gans 1975). They can move through dense vegetation with the speed and agility of snakes, but are not as mobile on smooth or sandy surfaces (personal observations). The strongly expressed serpentiform body of genus *Chamaesaura* gives the impression that these lizards should be active foragers. Indeed, actively foraging lizards are often slender with long, thin tails while sit-and-wait foragers tend to be stocky and have short tails (Vitt & Congdon 1978; Huey & Pianka 1981; Vitt & Price 1982).

The question arises whether or not sit-and-wait foraging in a grass habitat will require such pronounced body-elongation and limb-reduction as observed in *Chamaesaura*. In the family Gerrhosauridae, which is the sister family of the Cordylidae (Lang 1991), and which are classified as active foragers, similar snake-like forms are to be found (genus *Tetradactylus*). These forms occur sympatrically with members of *Chamaesaura* on grass-covered mountain slopes (Branch 1998). If *Tetradactylus* species are indeed active foragers, and the results of this study confirm that *Chamaesaura* species are sit-and-wait foragers like other members of Cordylidae, then the selective pressures leading to body elongation and limb reduction in the two genera may be completely different.

Chamaesaura anguina occurs along the southern and eastern coastal regions of South Africa, especially on gentle mountain slopes (Lang 1991; Mouton & Van Wyk 1997; Branch 1998). Studying the foraging biology of *C. anguina*, will give an indication of the foraging mode followed by the genus *Chamaesaura* in general. Three criteria were used to infer foraging mode: (1) the number and duration of movements related to foraging, quantified as the MPM and PTM; (2) the amount of tongue-flicks directed at different odours as a measure of prey chemical discrimination; (3) the stomach contents of individuals as an indication of their natural diet. Due to the fact

that sit-and-wait foragers mostly wait for prey to come to them, one expects the prey to be diurnally active invertebrates (Stamps 1977).

1.2 MATERIALS AND METHODS

1.2.1 MPM and PTM

1.2.1.1 Specimen collection: Twelve specimens of *Chamaesaura anguina* were collected on the slopes of Landdroskop in the Hottentots Holland Mountains, Western Cape, during April 1999. The snake-like morphology and cryptic coloration made observation of these lizards impossible in the wild and observations had accordingly to be made in semi-natural outdoor- and indoor experimental environments. A fluorescent non-toxic paint was used to mark each lizard with a different colour code to facilitate observation and identification.

1.2.1.2 Outdoor enclosure: Some of the variables created by laboratory conditions were eliminated by the use of an outdoor enclosure for making observations. An area close to the University of Stellenbosch, but similar to the grass habitat of Landdroskop, where the study animals were initially collected, were chosen for the construction of the outdoor enclosure. The Duthie Reserve was selected for this purpose. The outdoor enclosure (Figure 1.1) covered a surface of 16 m^2. The walls of the enclosure, made of plastic fly screen supported by steel droppers, were 1 m high. All the grass tufts touching the sides of the enclosure were removed to prevent the lizards from escaping. A strip of cardboard, 0.2 m high, was placed around the base of the cage so that the lizards could not see through the fly screen. Six lizards were placed in the enclosure and were allowed a period of seven days to adapt to their new environment. To prevent unnecessary distractions that might influence the lizards' behaviour, all observations

were made with a pair of binoculars from an observation tower, 4 m high. Due to the fact that the lizards were kept in an outside environment, dew and naturally occurring invertebrates supplied the water and food they needed to survive. This prevented the unnatural situation of having water and food points within the enclosure. Forty hours over a period of three weeks were spent observing the animals. Observations were restricted to sunny days at times when the lizards were active. Lizards were considered active when they positioned themselves in the upper reaches of the grass tufts, or when they were actively moving around in the enclosure.

1.2.1.3 Indoor enclosure: The six remaining lizards were observed in an observation room under regulated laboratory conditions for forty hours over a period of three weeks. The floor of the observation room, covering an area of 8 m^2, was covered with sand and grass tufts, thereby imitating a grass/restio habitat (Figure 1.2). A one-way glass panel made it possible to observe the animals without unnecessary distractions. Ambient temperature was regulated between 15 °C at night and 28 °C during the day. The lizards were fed a diet of grasshoppers (*Locusta migratoria*), house crickets (*Archeta domestica*) and mealworms (*Tenebrio* larvae). The grass was sprayed with water each morning and evening. Natural light reached the observation room through a large window, and six overhead spotlights provided additional illumination. The lizards were acclimatized to laboratory conditions for a period of seven days before the experimental period began.

1.2.1.4 Experimental procedure: The number and duration of movements relating to foraging, quantified as movements per minute (MPM) and the percentage of time spent moving (PTM), were the main criteria that were studied. The lizards in both the

Figure 1.1. Outdoor enclosure with observation tower to minimize disturbance during observations.

Figure 1.2. Indoor enclosure provided with grass tufts and a one-way glass panel.

outdoor and indoor enclosures were monitored for periods of 10 min each with the help of a stopwatch. Their transitions between moving and remaining stationary were recorded by means of a microcassette tape recorder, and were later transcribed to data sheets, following Cooper *et al.* (1997). A movement was defined as the act when an individual displaced itself physically by at least half its own body length. It was assumed that these movements were foraging related. Pauses of two or more consecutive seconds were recorded as periods of immobility (Cooper *et al.* 1997). The values obtained were compared with MPM and PTM values obtained for other lizard species from other studies to determine where *C. anguina* fitted into the continuum between sit-and-wait and active foraging. Statistical analysis of the data included determining the mean, standard error and range of the MPM and PTM values. The borders for MPM and PTM values are arbitrary, but a PTM of < 10 % and a MPM value of < 1.00 were accepted as indicative of a sit-and-wait foraging strategy (Perry 1995).

During the course of the observation period, special attention was given to the position of the lizard's body and tail when it captured its prey. Although observations were not quantified, those bearing directly on the interpretation of foraging mode are discussed:

1.2.2 Prey chemical discrimination

The ability of nine *C. anguina* lizards to detect prey odours and discriminate among prey and non-prey odours, was examined. Eight lizards were housed in pairs, and the remaining one singly, in glass terraria (600 x 400 x 300 mm) in a temperature controlled room for the duration of this study. Temperatures were regulated at 28 °C during the day, and were allowed to follow ambient temperature at night. Grass tufts were placed in each terrarium and water was available *ad libitum*. Lizards were kept in the terraria

for three weeks before the beginning of the experiment, and all were readily eating mealworms from the hand-held forceps without hesitation. To ensure responsiveness to prey during the study, they were not fed for one week prior to the experiment.

Responses of the lizards to three stimuli were observed: chemical stimuli derived from mealworms served as prey odours, distilled water served as an odourless control stimulus, and cologne served as a pungency control to determine their reaction to an odour which has no trophic relevance (Cooper 1990a). To prepare stimuli, cotton-tipped applicators were wetted with the distilled water. Prey stimuli were prepared by repeatedly rubbing the wet applicator over mealworm surfaces until it was slightly brown, while the applicator was dipped in diluted (1:1) cologne (English Leather) to prepare the pungency control. Odours were presented in a counterbalanced order, where each lizard responded to each stimulus once in a randomised block design.
A trial began with the experimenter slowly approaching a terrarium and carefully removing the lid. The cotton-tipped applicator bearing an odour was positioned 2-3 cm anterior to the lizard's snout. All tongue-flicks in a 60 s period, beginning with the emission of the first tongue-flick directed at the applicator, or until the lizard bit the applicator, were counted. If a lizard did not tongue-flick within 30 s in the trial, the experimenter briefly brought the applicator into contact with the lizard's snout. A mealworm was given to each lizard at the conclusion of the experiment to ensure that a lack in responsiveness to chemical stimuli was not due to satiation. All chemical discrimination trials for *C. anguina* were done on the same afternoon in October 1999.

1.2.3 Stomach contents

Twenty-one *Chamaesaura anguina* specimens, including representatives of every season, were available for dissection. They were collected throughout the year in the

Western Cape from June 1999 until April 2000 and fixed in formalin within 24 hours after capture. The stomach, small intestine and hind-gut (rectum) of each lizard were removed by opening specimens with a single mid-ventral incision, and preserved in 70% ethanol for later identification of food contents. The gut contents of each lizard were examined under a dissecting microscope and the number of each prey type, identified to lowest possible taxonomic category (usually family), was determined. Furthermore, prey was specifically noted to be either diurnally or nocturnally active.

1.3 RESULTS

1.3.1 MPM and PTM

Low MPM and PTM values were recorded for *Chamaesaura anguina* (Table 1.1). Ninety-three percent of recorded moves were of less than six seconds duration. The MPM for the lizards in the outdoor enclosure ranged from 0 - 0.70, with a mean of 0.38 ± 0.17 SD (N = 4; two of the six lizards were never seen foraging), while for those in the indoor enclosure, it ranged from 0.10 - 0.60 with a mean of 0.37 ± 0.08 SD (N = 6). The range of the PTM for the specimens in the outdoor enclosure was 0 - 2.83 %, with a mean of 1.71 % ± 0.64 SD, while for the indoor enclosure the PTM range was 0.67 - 3.50 % with a mean of 2.14 % ± 0.44 SD. Values obtained in the indoor and outdoor enclosures did not differ significantly (MPM vs. MPM, $df = 9$, $t = -0.05$, $P = 0.96$; PTM vs. PTM, $df = 9$, $t = 0.58$, $P = 0.58$) and were pooled. The MPM (0.37 ± 0.21) and PTM (1.92 % ± 0.93 SD) values recorded for *C. anguina* (N = 10) were respectively lower than 1.00 and 10 %.

It was further observed that *C. anguina* is highly visually orientated, positioned horizontally or vertically in the grass tufts with the body slightly bent, for long periods during the day. Usually only their heads stuck out of the tuft, but they were also

Table 1.1. Movements per minute (MPM) and percentage of time moving (PTM) of three lizard families presented as mean ± 1.0 SE and range. SW - sit-and-wait forager; AF - active forager; n.a. - not available. Criteria for SW was a MPM of < 1.0 and a PTM of < 10 % (following Perry 1995).

Species	Foraging mode	MPM		PTM (%)	
		Mean ± SE	Range	Mean ± SE	Range
Lacertidae ✶					
Eremias lineoocellata	SW	1.54 ± 0.24	n.a.	14.30 ± 3.00	n.a.
Eremias lugubris	AF	2.97 ± 0.28	n.a.	57.40 ± 3.80	n.a.
Meroles suborbitalis	SW	1.83 ± 0.19	n.a.	13.50 ± 1.60	n.a.
Eremias namaquensis	AF	2.78 ± 0.31	n.a.	53.50 ± 5.20	n.a.
Ichnotropis squamulosa	AF	3.10 ± 0.14	n.a.	54.60 ± 7.90	n.a.
Nucras tessellata	AF	2.90 ± 0.37	n.a.	50.20 ± 5.20	n.a.
Gerrhosauridae #					
Cordylosaurus subtessellatus	AF	1.20 ± 0.02	1.00-1.39	47.40 ± 8.10	39.33-55.50
Gerrhosaurus validus	AF	0.65 ± 0.17	0.48-0.82	14.90 ± 11.7	3.20-26.50
Cordylidae #					
Platysaurus capensis	SW	1.27 ± 0.32	0.00-6.82	6.62 ± 1.58	0.00-24.17
Pseudocordylus capensis	SW	0.59 ± 0.20	0.00-1.11	6.77 ± 2.00	0.00-14.06
Pseudocordylus microlepidotus	SW	0.00 ± 0.00	n.a.	0.00 ± 0.00	n.a.
Cordylus imkae	SW	0.00 ± 0.00	n.a.	0.00 ± 0.00	n.a.
Cordylus polyzonus	SW	0.04 ± 0.02	0.00-0.34	0.15 ± 0.07	0.00-1.00
Cordylus cordylus	SW	0.09 ± 0.02	0.00-0.70	0.27 ± 0.08	0.00-2.50
Cordylus niger	SW	0.09 ± 0.03	0.00-0.60	0.19 ± 0.06	0.00-1.33
Cordylus cataphractus +	SW	0.23 ± 0.08	0.00-0.96	2.20 ± 0.71	0.00-7.19
Chamaesaura anguina ⊗		0.37 ± 0.21	0.00-0.70	1.92 ± 0.93	0.00-3.50

✶ Values taken from Huey and Pianka (1981)
\# Values taken from Cooper *et al.* (1997)
\+ Value taken from Mouton *et. al.* (1999)
⊗ This thesis

observed to lie on the ground next to or nearby grass tufts. Prey capture usually consisted of a rapid approach, followed by a quick strike. Most of the time the lizard kept its elongated tail entangled in the grass. Depending on the site of prey capture, the lizard either stayed at the site, returned to the previous location, or moved to another elevated site. Locomotion was mainly restricted to the strike action.

1.3.2 Prey chemical discrimination

After failing the test for normality and homogeneity of variance of the data, a test of significance was conducted by means of a Kruskal-Wallis One Way ANOVA on ranks for a single-factor experiment having repeated measures (Sigma-Stat 2.0 by Jandel). Differences among responses to the odours were accepted as significant when $P < 0.05$. Eight of the 27 trials showed a tongue-flick score of 0. No individual attacked the odour-bearing cotton applicator during a trial. The results show that no statistically significant difference existed among the three treatment groups (Kruskal-Wallis; $H = 2.41$, $df = 2$, $P = 0.30$). Means and SD in response to mealworm odour were 4.33 ± 3.97, to cologne 5.11 ± 3.95, and to deionized water 2.56 ± 4.36 (Table 1.2). All the lizards ate mealworms presented at conclusion of trials.

1.3.3 Stomach contents

Five of the stomachs ($N = 21$) examined contained no prey items. Analysis of the stomach contents of the remaining 16 lizards revealed that the diet of *Chamaesaura anguina* was solely made up of arthropods (Arachnida, Blattodea, Coleoptera, Hemiptera, Mantodea, Orthoptera, Odonata and Symphyla). Frequencies of ingested prey items are presented in Table 1.3. A wide spectrum of prey items was found

Table 1.2. The response of *Chamaesaura anguina* (N = 9) to three odours on cotton-tipped applicators: mealworm odour, cologne and deionized water (dH_2O). *Mean TF/min* = number of tongue-flicks in one minute; *attack* = number of times individuals bit the odour-bearing applicator.

	Mealworm odour	**Cologne**	**dH_2O**
Mean TF/min	4.33	5.11	2.56
SE	3.97	3.95	4.36
Range	0.0 - 9.0	0.0 - 13.0	0.0 - 12.0
Attack	0	0	0

Table 1.3. Frequency of occurrence of prey items found among stomach contents of *Chamaesaura anguina*, expressed as a percentage of the total number of stomachs (N = 16) that contained a particular prey item.

Prey items (order, family)	**Frequency of occurrence (%)**	**Activity (Diurnal vs. Nocturnal)**
ARACHNIDA (spiders)	25.00	Diurnal
BLATTODEA (cockroaches)	12.50	Nocturnal
COLEOPTERA (beetles)	**68.75**	
Alticinae	25.00	Diurnal
Bostrychidae	12.50	Diurnal
Chrysomelidae	12.50	Diurnal
Curculionidae	6.25	Nocturnal
Unknown	12.50	Unknown
HEMIPTERA (leafhoppers)		
Cicadellidae (Cephalelus sp.)	6.25	Diurnal
MANTODEA (preying mantids)	6.25	Diurnal
ODONATA (damselflies)		
Zygoptera	6.25	Diurnal
ORTHOPTERA (grasshoppers & crickets)	**62.50**	
Acrididae	31.25	Diurnal
Pamphagidae	6.25	Diurnal
Tettigoniidae	25.00	Diurnal
SYMPHYLA (symphylans)		
Scutigerellidae	6.25	Nocturnal

ranging from spiders to damselflies, but stomach contents mainly consisted of species from orders Coleoptera (68.75 %) and Orthoptera (62.50 %). Most apparent was the diurnally surface active insects, while only 7.69 % of all ingested invertebrates were nocturnal. No plant material was found in the stomach samples. Parasites were quite abundant with 50 % of the lizards infected either with nematodes, flatworms or both.

1.4 DISCUSSION

1.4.1 MPM and PTM

The seven cordylid species studied by Cooper *et al.* (1997), representing the genera *Cordylus, Pseudocordylus* and *Platysaurus*, were all reported to be sit-and-wait foragers. Compared to its fellow cordylids, it is clear that *Chamaesaura anguina* fits the criteria for a sit-and-wait forager. MPM and PTM values obtained for the lizards in both the outdoor and the indoor enclosures, are clearly lower than those obtained for some members of the Gerrhosauridae, which are classified as active foragers. The difference between the MPM values obtained for the outdoor enclosure and the indoor enclosure was minimal, suggesting that the conditions under which the study were conducted, did not have an influence on the foraging behaviour of the specimens. The MPM-values classifying two *Gerrhosaurus* species as active foragers (Table 1.1), according to Cooper *et al.* (1997), were similar to the MPM-values recorded for some lacertids, classified as sit-and-wait foragers by Huey & Pianka (1981). It seems therefore that the ranges for MPM tend to overlap. PTM values are more clear-cut and no overlaps of ranges occur in Table 1.1. The PTM values recorded for *C. anguina* in the outdoor- and indoor enclosures are fairly similar, although the lizards tended to move around for longer periods in the laboratory observation room. The reason for this may have been the higher prey density in the indoor enclosure provided to them during

the study period. However, the MPM and PTM values fall well inside the sit-and-wait borders of MPM < 1 and PTM < 10 %.

Different search strategies require certain morphological adaptations to facilitate particular capture techniques (Moermond 1979). The efficiency of a morph in a particular habitat is dependent on its ability to hunt in that certain microhabitat or patch (Moermond 1979). The *Cordylus* species listed in Table 1.1 all spend most of their time sitting motionless, usually on the top of rocks from which they can scan relatively large areas (Cooper *et al.* 1997). These lizards usually capture prey from ambush, sometimes rushing off the rocks to the ground to the attack and then return to the rocks to continue with their visual search (Cooper *et al.* 1997). *Chamaesaura anguina* feeds in much the same way as the other rock-dwelling cordylids. The importance of visual cues while searching for prey explains why the lizards were usually found in an elevated position when active. While perching in the grass, the elongated body has to be bent to distribute weight effectively. The reduced limbs are tucked against the body during undulatory propulsion, but usually extended to further distribute weight during times of waiting while feeding.

1.4.2 Prey chemical discrimination

All members of the Cordylidae, which have been tested to date, lack prey chemical discrimination (Cooper 1994; Cooper & Van Wyk 1994; Cooper *et al.* 1997; Mouton *et al.* 1999), and *Chamaesaura anguina* seems to be no exception. The fact that no significant differences were found between the number of tongue-flicks emitted to the three different chemical stimuli supports the possibility that *C. anguina* does not have the ability to discriminate among different odours. This verifies the prediction that this lizard is indeed a sit-and-wait forager. Lizards exhibiting the sit-and-wait foraging

strategy relies almost exclusively on visual orientation (Stamps 1977), and lack the ability to discriminate between prey and non-prey odours (Cooper 1989, 1990b, 1992, 1994a, b; Cooper & Van Wyk 1994). Foraging mode, as well as prey chemical discrimination ability, is reported to be stable within most lizard families (Garland & Losos 1994; Cooper 1995), and the results of this study for *C. anguina* show that this is probably also true for the Cordylidae.

1.4.3 Stomach contents

According to Huey & Pianka (1981), sedentary and patchily scattered prey is more likely to be detected by actively foraging predators through chemical cues and active searching. In contrast, sit-and-wait foragers should encounter and consume more diurnally active and mobile prey due to their heavy reliance on visual cues, where prey movement usually is a prerequisite for detection (Huey & Pianka 1981; Mouton *et al.* 1999). The prey types found in the stomachs of the 21 *Chamaesaura anguina* examined mainly comprised diurnally active arthropods (Table 1.3), thereby confirming the assumption that this species follows a sit-and-wait strategy. Generally, the diet was dominated by Coleoptera (beetles) and Orthoptera (grasshoppers and crickets). Beetles comprise the largest order of insects, inhabiting almost all the world's environments, while order Orthoptera includes some of the largest living insects (Scholtz & Holm 1985; Brusca & Brusca 1990). Both are groups of highly active insects either flying, jumping or crawling around (Scholtz & Holm 1985).

The presence of a symphylan (family Scutigerellidae), a cockroach and a snout-beetle in the stomach contents, however, suggests that sedentary and nocturnal insects are also preyed upon, even though it made up only a small part (7.69 %) of the diet of *C. anguina*. Symphylans are small, soft, uncalcified and eyeless insects that occur in soil

and rotting vegetation (Brusca & Brusca 1990) (like at the base of a grass tuft), where the lizard most probably found it. Nocturnal insects are sometimes active during the day as well (Brusca & Brusca 1990), but they may have been caught by the lizards while hiding in the dense grass while waiting for nightfall. No seasonal variation in diet was recorded, though this may be due to the small sample size. The data suggest an opportunistic approach to foraging that enables *C. anguina* to take advantage of sedentary or nocturnal prey that hide in the bottom of grass tufts, as well as prey that are diurnally active in other parts of the vegetation.

Fire can have extreme effects on the habitat structure and plant species combination (Collins & Gibson 1991), which in turn has the effect to influence a reptile community through changes in food supply (Warren *et al.* 1987; Cavitt 2000). Three of the five collected lizards with empty stomachs, together with three other lizards with stomachs containing only a few prey items, were gathered five months after a veld fire destroyed huge parts of the mountain vegetation where these lizards occur. During this time the veld had not sufficiently recovered, and the sparsely distributed grass tufts hampered undulatory locomotion of *C. anguina* lizards. For this entire period these lizards were confined to a small area of a few unburnt grass tufts, and most probably suffered from starvation due to the insect shortage after the fire. Due to the dependence of *C. anguina* on habitat structure for locomotional, foraging and safety purposes, habitat destruction could have a profound effect on the survival of this species. Even though fire induced changes of the physical structure of habitat are favourable to some lizard species that prefer open habitats for foraging (Griffiths & Christian 1996), it could be very unfavourable to others that are confronted with increased exposure, temperature fluctuations and altering insect abundance (Mushinsky 1992, Cavitt 2000).

1.4.4 Summary and conclusions

Foraging mode seems to influence many aspects of the lives of lizards, and may even be related to the evolution of body shape (Huey & Pianka 1981). Morphological and behavioural traits associated with search movements and prey capture are expected to enhance the success of a particular hunting pattern (Kiester *et al.* 1975). While foraging, the elongated tail makes it possible for *Chamaesaura anguina* to position itself in the upper reaches of the tufts. The reduced limbs, when extended, also contribute to distribute weight. The elongated body and tail required for lateral undulation, may not play such a big role in locomotion while foraging, seeing that a sit-and-wait forager remains inactive for long periods of time, but is very helpful in times when a quick escape is necessary. No definite places of retreat are available in the grass microhabitat, and when threatened by fire, fleeing might be the only survival option (Boycott 1990). Furthermore, *C. anguina* uses its elongated body and tail to launch at its prey from one grass tuft to another, almost in the same way that a chameleon uses its elongated tongue. Having an elongated body and reduced limbs in a grass habitat might be advantageous, even for a sit-and-wait forager.

The low MPM and PTM values, the lack of prey chemical discrimination ability, and the stomach contents recorded for *C. anguina*, suggest that members of the genus *Chamaesaura* follow a sit-and-wait foraging strategy.

CHAPTER TWO

TEMPERATURE PREFERENCE, MOVEMENT PATTERNS AND MICROHABITAT USE IN THE CAPE GRASS LIZARD, *CHAMAESAURA ANGUINA*

2.1 INTRODUCTION

Despite the fact that lizards are obligatory ectotherms, thermoregulation studies produced convincing evidence that many reptiles behaviourally maintain a preferred body temperature (Soulé 1963; Schall 1977; Fuentes & Jaksic 1979). Their ability to do so, even in environments with wide diurnal heat fluctuations, depend largely on the usage of regulatory behaviours and postural modifications that control heat exchange with the environment (Huey 1982; Bauwens *et al.* 1990; Bauwens *et al.* 1999). A lizard's preferred body temperature is a reflection of its overall geographical distribution, and knowledge of thermal relationships with the environment can provide an integrative overview of the general ecology of certain species (Pianka & Parker 1975; Schall 1977). High altitude lizards often have lower preferred body temperatures falling in greater thermal ranges than conspecific or congeneric populations occurring at lower elevations (Soulé 1963; Bauwens *et al.* 1990; Bauwens *et al.* 1999).

The family Cordylidae encompasses a remarkable, but poorly studied segment of the saurian fauna of southern Africa. Members of the genus *Chamaesaura* are characterized by a relatively peculiar combination of morphological and ecological adaptations that tend to set them apart from the other genera of this family. In fact, it is formally placed in a separate subfamily, Chamaesaurinae, the other genera belonging to the Cordylinae. Unlike most other cordylids, which are rock-dwelling, *Chamaesaura* species are grass-living, occurring in grassland and restio habitats (Branch 1998).

Furthermore, the three species in this genus all have elongate, snake-like bodies with minute fore- and hind limbs (Branch 1998). The aim of this study was firstly to determine the preferred body temperatures of the Cape grass lizard, *Chamaesaura anguina*, as a representative of the elongated forms in this genus.

The second aim of the study was to report on movement patterns and microhabitat-use exhibited by *C. anguina*. Rock-dwelling cordylids shelter underneath rocks and in crevices during times of inactivity or threat, and individuals of these species may occupy specific rocks or crevices for extended periods of time, even years (Mouton & Van Wyk 1997; Branch 1998). The rocky habitat provides a wide array of safe retreats near or next to the lizard's perch, so even though the lizards are exposed for prolonged periods during sit-and-wait feeding, the availability of safe retreats prevents significant predator impact on the species (Mouton & Van Wyk 1997). Except for snakes, almost all limbless forms are shelterers or burrowers (Gans 1975), but according to Branch (personal communication), nobody has ever claimed finding a *C. anguina* lizard sheltering in a burrow, crevice or underneath a rock. *Chamaesaura anguina* is not only habitat specific, but refuge specific as well, by using only grass tufts as shelter (personal observation). Therefore, it is not expected that this species will show the same reliance on specific shelter sites, as displayed by the rock-dwelling cordylids. Such information may be important in understanding possible impacts of predators and veld fires on populations.

Information is limited on how *Chamaesaura* captures its prey and uses its broken environment to its foraging advantage. Foraging mode of an animal is an important factor in understanding its interactions with the environment, and might even be related to the evolution of anti-predator behaviour (Vitt 1983), morphology and physiology (Huey & Pianka 1981). In general, sit-and-wait foragers remain in one

location for some time, normally relying heavily on visual detection of prey and often making use of elevated perches to increase their field of vision (Bissinger & Simon 1979; Stamps 1983; Cooper 1994b). It is therefore expected, being part of a sit-and-wait foraging family, that *Chamaesaura* will position themselves on top of the grass tufts, waiting for passing prey. Although they will be more exposed to predators, such a position will allow rapid escape by "grass-swimming" in case of danger. The lateral undulatory locomotor method, as used by *C. anguina*, is probably more effective than quadrupedal movement in terms of energy to maintain a given velocity (Chodrow & Taylor 1973), and the snake-like body of the lizard makes movement in such an environment easy and energetically cheap (Gans 1975).

2.2 MATERIALS AND METHODS

2.2.1 Study animals

Twelve *Chamaesaura anguina* lizards were collected on the slopes of Landdroskop in the Hottentots Holland Mountains, Western Cape, during April 1999. They were transported to the University of Stellenbosch where they were initially kept in pairs in 400 x 600 x 300 mm glass terrariums supplied with grass tufts. Heat was provided by 40 W spotlights and water and food (*Tenebrio* larvae) were available *ad libitum*. The snake-like body and cryptic colouration of these lizards made studying them in the wild an impossible task. Observations had accordingly to be made in semi-natural environments. Parts of the body and tail were painted with non-poisonous fluorescent paint to facilitate identification and to make them more conspicuous to the observer.

2.2.2 Preferred body temperature

2.2.2.1 Experimental setup: Temperature preference was determined in a temperature-controlled room under regulated laboratory conditions. A terrarium (2.0 x 2.0 x 0.6 m) was supplied with sand and grass tufts. A thermal gradient within the terrarium was established in the air-conditioned room, regulated at 16 °C, with two spotlights (500 W each) placed in one corner of the terrarium, following Christian & Weavers (1996). This provided a continuous thermal gradient as indicated by floor temperatures that ranged from 16 °C in the corner furthest from the spotlights, to 45 °C in the part of the terrarium directly underneath the spotlights. Two overhead fluorescent tubes provided additional illumination. The lizards were fed on a diet of house crickets (*Archeta domestica*) and mealworms (*Tenebrio* larvae). The grass was sprayed with water each morning and evening.

2.2.2.2 Experimental procedure: Four *Chamaesaura anguina* specimens were placed in the terrarium and allowed a 24 h acclimatization period. It was assumed that, during peak lizard activity, they would maintain their body temperature within their preferred range. Lizards were considered to be active when their heads stuck out of the grass tufts, when they were lying next to, or in, the upper reaches of the tufts, or when they moved around in the terrarium. On six occasions over the following two days, during peak lizard activity, the body temperature of each lizard was taken quickly on capture using a copper-constantan thermocouple that was inserted 1 cm deep into the cloaca. To prevent the examiner's temperature influencing that of the lizard, it was held behind the head and handled minimally while measurements were taken. The mean body temperature for each individual was calculated, as well as the mean preferred body

temperature for the species. The experiment was repeated three times, each time with a different set of four lizards.

2.2.3 Movement patterns and microhabitat use

2.2.3.1 Experimental setup: Some of the variables created by laboratory conditions were eliminated by the use of an outdoor enclosure for making observations. I refer to Chapter 1, paragraph 1.2.1.2, for details concerning the construction of the outdoor enclosure.

2.2.3.2 Experimental procedure: The position of all the grass tufts in the outdoor enclosure, which was divided into a grid with four segments, were mapped (Figure 2.2). Every morning, for a period of 17 consecutive days, the position of each lizard within the enclosure was noted on the map. Therefore, each lizard had a maximum of 16 opportunities to change refuge site. These observations were made at 08h00, before lizard activity started. The use of the micohabitat for shelter purposes during times of inactivity was recorded while noting their positions in the enclosure. A lizard's specific manner of sheltering or hiding within the grass tuft was also recorded.

For each lizard, the number of times that it changed refuge site, as well as the number of times it returned to the same refuge site, was expressed as a percentage of the maximum number of times that it could change refuge site. The range, covered by each lizard within the limits of the enclosure, was determined by measuring the distance between the two furthest refuge sites.

Further observations on microhabitat use were made from the observation tower and were restricted to sunny days at times when the lizards were active. A total number of 40 hours over a three week period were spent on observation. Lizards were

Figure 2.1. The oudoor enclosure that housed six *Chamaesaura anguina* lizards for observational purposes.

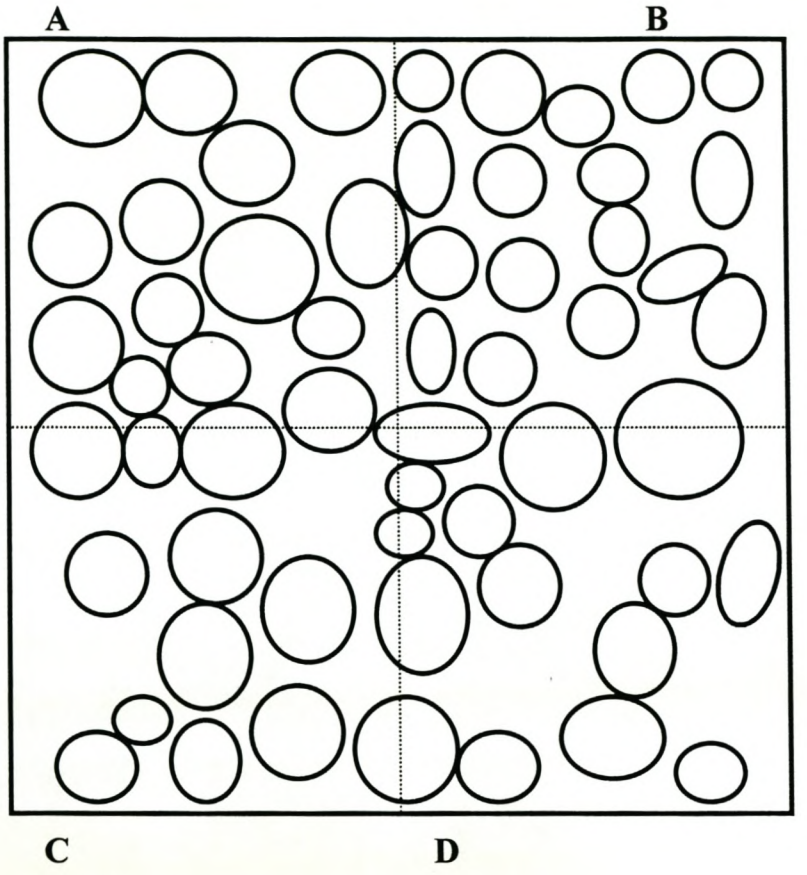

Figure 2.2. Map of the oudoor enclosure showing the positions of the grass tufts in four quadrates.

considered active when they positioned themselves in the upper reaches of the grass tufts, or when they were actively moving around in the enclosure. These observations are purely descriptive.

2.3 RESULTS

2.3.1 Preferred body temperature

A total of 72 body temperature measurements were taken from the twelve lizards. Figure 2.3 displays the measured body temperatures of the *Chamaesaura anguina* individuals, ranging from 22.62 °C - 27.07 °C with a mean of 24.82 °C ± 2.27.

2.3.2 Movement patterns and microhabitat use

Not all the lizards in the outdoor enclosure were located every morning during the 17 day observation period. Each lizard was located on average 14.5 times. Although other options such as rodent burrows and rocks were available in the enclosure, the lizards never sheltered in them. Only grass tufts were used as refuge sites. Only 16 of the 62 available grass tufts were used as refuges during times of inactivity. There were significant differences between the average heights (student's *t*-test; $P < 0.05$) and diameters (student's *t*-test; $P < 0.05$) of the grass tufts that were used as refuge sites and those tufts that were not. The mean height of the grass tufts used as shelters, was 0.58 m ± 0.08 SD (range 0.43 - 0.72 m), while the tufts not used as shelters, had a mean height of 0.38 m ± 0.01 SD (range 0.17 - 0.64 m). The mean diameter of the refuge grass tufts was larger, 0.43 m ± 0.14 SD (range 0.24 - 0.66 m) than the mean diameter of the unused grass tufts, 0.30 m ± 0.09 SD (range 0.18 - 0.61 m). There was a significant difference between the heights (student's *t*-test; $P < 0.001$) and the diameters (Mann-Whitney Rank Sum test; $P < 0.001$) of the used and the unused grass tufts

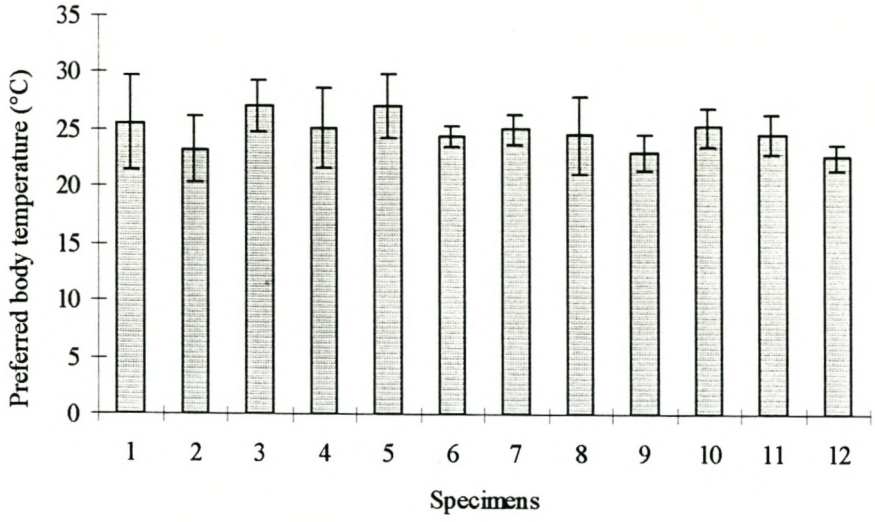

Figure 2.3. Graph of the mean preferred body temperatures (°C), with error bars, measured for the twelve *Chamaesaura anguina* individuals.

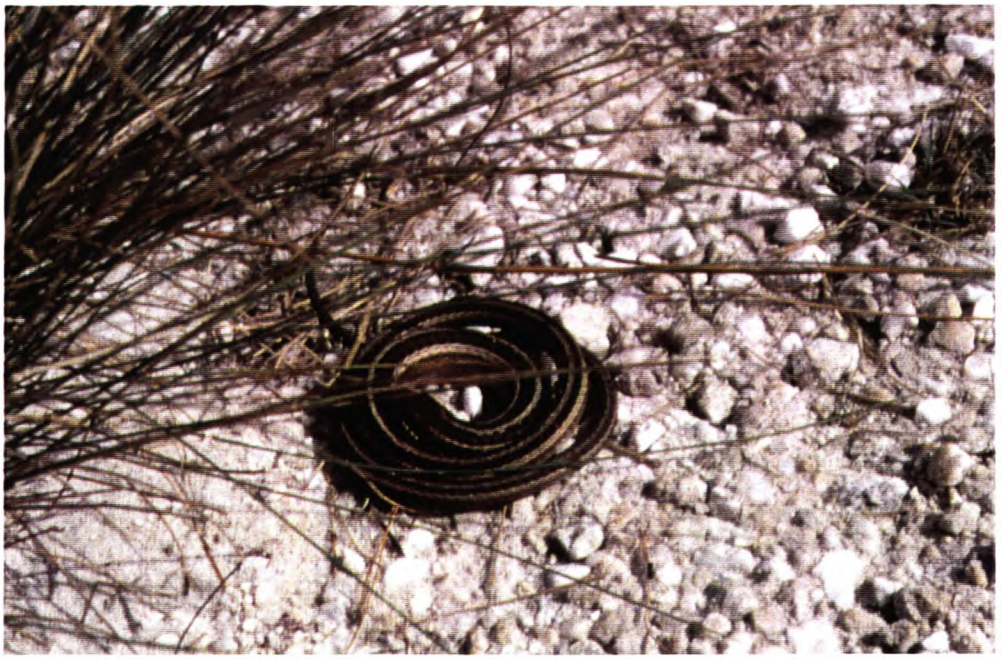

Figure 2.4. A *Chamaesaura anguina* lizard in a coiled-up position.

respectively. One section of the enclosure was avoided by the lizards (quadrate B in Figure 2.2). In 91.67 % of the cases the lizards were found coiled up at the bottom in the center of a grass tuft (Figure 2.4). On eight occasions the lizards were found lying horizontally, only slightly coiled up, at the bottom of a grass tuft. On five occasions, two lizards were found coiled up together in the same grass tuft.

Refuge changes occurred on an average of 44.75 % (N = 39) of the times that were available for the lizards to make location changes. After the lizards changed refuge site, they returned to the same refuge location or grass tuft on an average of 12.02 % (N = 39) of the total number of location changes that were made. The mean range diameter within the limits of the 16 m^2 enclosure was 2.83 m ± 0.38 SD (N = 6). The maximum period that a lizard stayed at one refuge location was eight days.

It was observed that *Chamaesaura anguina* was in an elevated position for long periods of the day, positioned horizontally or vertically in the grass tuft with the lizard's body slightly bent in a S-shaped curve. Usually only the head stuck out of the tuft. They were also observed to lie on the ground next to the tufts. Prey capture usually consisted of a rapid approach, followed by a quick strike. Most of the time, the lizard kept its elongated tail entangled in the grass. Depending on the site of prey capture, the lizard either stayed at the site, returned to the previous location, or moved to another elevated site. Locomotion was mainly restricted to the strike action.

2.4 DISCUSSION

The preferred body temperature determined for *Chamaesaura anguina* (25°C) is lower than that recorded for other cordylid species: *Cordylus macropholis* has a preferred body temperature of 28 - 29°C (Bauwens *et al.* 1999), *C. vittifer* 32.1 °C (Skinner 1991), *C. tropidosternum jonesi* 33.5 ° C (Wheeler 1986), and *Pseudocordylus capensis*

31.3 °C, *P. nebulosus* 30.6 °C, *C. polyzonus* 32.5 °C, *C. cordylus* 32.2 °C, *C. oelofseni* 31.4 °C, and *C. cataphractus* 32 °C (J.B. Losos, P. le F.N. Mouton, D. Bauwens and A.M. Castilla, personal observation). It is difficult to determine whether the relatively low temperature preference of *C. anguina* is due to flaws in the experimental procedure, or whether it represents a characteristic of this terrestrial cordylid. Implicit in this approach of measuring preferred body temperature, is the assumption that the lizards in the laboratory thermoregulate by optimally exploiting the available thermal environment. This means that the lizards' selected body temperatures represent the preferred body temperatures that they would choose in an ideal environment. The lizards might, however, not thermoregulate in this way, because they were suffering from stress or had a different thermoregulatory response to the artificial environment in the laboratory compared to the field. One *C. anguina* individual measured in the field for example, had a body temperature of 31.7 °C (Mouton, personal communication), which is higher than the body temperatures measured for most specimens during this study.

On the other hand, *C. macropholis*, usuallly sheltering among the branches of *Euphorbia caput-medusae* plants, also displays a relatively low preferred body temperature (Bauwens *et al.* 1999), while the rock-dwelling cordylids' all have a relatively higher preferred body temperature, above 30 °C. Lizards that stay under vegetative cover cannot take advantage of the full range of thermal conditions in their habitat (Bauwens *et al.* 1999), especially when associated with an extremely low frequency of movements. *Chamaesaura anguina* exhibits severely restricted microhabitat usage, retaining their positions in the grass for extended periods. Furthermore, this species occurs on the mountain slopes where temperatures are usually lower than in the lowlands. Lizards with reduced limbs always show a reduction in

body diameter with relation to body length compared to species with little or no reduction (Gans 1975). Elongated limbless lizards tend to be on the low-weight side of weight metabolism curves (Gans 1975). The obvious problem with elongated lizards is the increased surface-volume ratio (Pough 1980; Shine 1986). This means that the lizard gains heat more quickly at high temperatures, but also looses heat more rapidly at low temperatures. The combination of vegetative cover, high altitude, together with its high surface-volume ratio, possibly contributes to the low preferred body temperature found in *C. anguina*.

Chamaesaura anguina does not show the same reliance on specific shelter sites as other cordylids which live in rocky habitats. Not only were short term shifts in refuge sites observed, but the lizards were also very selective when choosing the grass tuft in which to shelter for the night. Only a few (16 of more than 50) of the available tufts were used during the observation period. These grass tufts were all taller with larger diameters than the unused ones. This could also be the reason why one of the quadrates in the cage was never used as a refuge area. All the grass tufts in the unused quadrate were on average shorter with smaller diameters than the tufts in the remaining quadrates. One can safely assume that the larger tufts provide better protection against predators during times of inactivity. Refuge location changes occurred often (44,75 %), but it was never observed that a lizard that was active during the day, returned to the same refuge location to shelter for the night. The mean distances that the lizards moved was quite extensive (2,83 m), keeping in mind that they were kept within the limits of a 4 x 4m enclosure. Ranges broadly overlapped with each other, but no cases of territorial defence were observed. During times of inactivity, *C. anguina* usually shelters in a coiled up position at the bottom in the middle of a grass tuft. By sheltering in a coiled-up position, it decreases its surface-volume ratio, preventing it to loose too

much of its own body heat. This may explain why they demonstrated this behaviour especially on the colder nights. Sometimes the lizards coiled-up when they were threatened as well.

The efficiency of a morph in a particular habitat is dependent on its ability to hunt in that certain microhabitat or patch (Moermond 1979). *Cordylus* species studied to date are all sit-and-wait foragers, spending most of their time sitting motionless, usually on the top of rocks from which they can scan relatively large areas (Cooper *et al.* 1997). These lizards usually capture prey from ambush, sometimes rushing off the rocks to the ground to attack and then return to the rocks to continue with their visual search (Cooper *et al.* 1997). *Chamaesaura anguina* forages in much the same way as the other rock-dwelling cordylids. The sit-and-wait foraging strategy is highly related to visual orientation on which these type of foragers almost exclusively rely (Stamps 1977). This explains why *C. anguina* was usually found to forage in an elevated position. While perching in the grass, the elongated body has to be bent to distribute weight effectively. The reduced limbs are tucked against the body during undulatory propulsion, but usually extended to further distribute body weight during times of waiting while foraging. During the quick strike when capturing its prey, the elongated tail sometimes acts as an anchor of support.

Characteristics like body and tail elongation with limb reduction, may seem contradictory to the expected morphology of a sit-and-wait forager, especially when keeping in mind that most elongated lizards are active foragers (Huey & Pianka 1981; Vitt 1983). Active foraging lizards appear to experience higher predation than sit-and-wait foragers (Vitt & Price 1982), which remain in one location for some time while searching visually for prey (Cooper 1994b). Tail elongation, commonly found in actively foraging species, may represent an adaptation against predation by increasing

the likelihood that a predator will grab the detachable, slender tail, leaving intact the rest of the lizard (Huey & Pianka 1981; Vitt 1983). If this is the case for *C. anguina*, loosing its tail in self-defence would mean loosing about two thirds of its own body length. This could have a negative influence on performing lateral undulation, where a long and slender body is a prerequisite, and hinder its chances to escape. Even though one of the specimens collected was without a tail, this phenomenon probably occurred as a last option when under threat.

2.4.1 Summary and conclusions

The low preferred temperature exhibited by *Chamaesaura anguina* might be attributed to the combined influence of vegetative cover, high altitude, and its high surface-volume ratio. Although *C. anguina* does not show reliance on a specific shelter site, the taller, broader tufts are generally preferred as refuge during inactivity. They usually shelter in a coiled-up position at the bottom in the middle of the grass tufts. *Chamaesaura anguina* forages from an elevated position by entangling its elongated body in the grass for efficient weight distribution.

CHAPTER THREE

REFUGE SELECTION AND SUSCEPTIBILITY TO FIRE IN THE CAPE GRASS LIZARD, *CHAMAESAURA ANGUINA*

3.1 INTRODUCTION

Fire is a frequent hazard in the southern African grassland and fynbos habitats (Cowling & Richardson 1995). Burning is widely used in southern Africa to 'modify' grasslands for agricultural use and to 'improve' stock grazing, especially in the highveld region of Swaziland and in the northeastern savanna of South Africa (Boycott 1990). Apart from the deliberately ignited fires, natural fires also occur frequently, especially in the southwestern fynbos regions (Cowling & Richardson 1995). On average, lightning alone in the Western Cape causes three to six major fires per year (M. Gentle, personal communication) and environmental factors such as frequent, strong winds together with hot, dry summers play a significant role in promoting the occurrence of veld fires in this area (Cowling & Richardson 1995).

Although fire causes extensive habitat modification in South Africa, its effect on the lizard fauna is not well documented (Stuart & Meakin 1983; Wright 1988; Boycott 1990; Baard 1997). Most evaluations of the effects of fire on vertebrates indicate that the major factor affecting survival is the harsh habitat change following the fire, rather than direct mortality during the fire itself (Erwin & Stasiak 1979; Mushinsky 1992; Cavitt 2000). Some species, however, may be more susceptible to fire because of certain aspects of their morphology, biology and behaviour (Fyfe 1980; Cavitt 2000).

There is a distinct relationship between morphology and habitat use among lizards, different morphologies functioning best in different habitats (Huey 1991; Garland & Losos 1994). Refuge selection is accordingly not only influenced by the array of refuge

options that a specific environment offers, but also by the morphology of the species inhabiting the area. The Cordylidae, a small family of lizards endemic to Africa, comprises mainly rock-dwelling species that spend times of inactivity or when threatened, underneath rocks or in crevices (Mouton & Van Wyk 1997; Branch 1998). Stocky, depressed bodies with well-developed limbs and relatively short tails characterize these lizards (Branch 1998). The impact of fire on these rock-dwelling species appears to be minimal in that the rocky environment provides a wide array of safe retreats (Baard 1997; personal observations).

In contrast to the other three genera of the Cordylidae, which comprise mainly rock-dwelling species, *Chamaesaura* is exclusively grass-living (Mouton & Van Wyk 1997; Branch 1998). All three species in this genus occur in escarpment and montane grasslands (Lang 1991; Mouton & Van Wyk 1997). Members of the genus differ markedly in morphology from other cordylids in displaying extreme diametric reduction, body and tail elongation and limb reduction (Mouton & Flemming 1999). Normally the tail is more than four times body length and makes locomotion by means of lateral undulatory movement possible (Gans 1975; personal observation). These diurnal lizards are exposed for extensive periods while basking and sit-and-wait feeding (personal observation), but unlike the rocky environment, the grass habitat does not offer well-defined retreats when danger threatens. Crypsis and immobility appear to be the primary defence strategies of these lizards, but these obviously cannot provide protection against fire.

Although grass and restioid habitats do not offer the same variety of retreats as a rock habitat, they normally contain at least some refuges such as rodent burrows and scattered rocks and other objects in which or underneath which, lizards can hide. The question is whether *Chamaesaura* species make use of such refuges, if available, to

spend times of inactivity or to retreat to when threatened by either predators or fire. *Chamaesaura anguina*, occurring along the southern and eastern coastal regions of South Africa (Branch 1998), was used as representative of the elongated forms of this genus.

Phylogenetic relationships in the Cordyliformes suggest that, within the Cordylidae, a rock-dwelling lifestyle is the primitive condition and a terrestrial/arboreal lifestyle, the derived one (Mouton & Van Wyk 1987; Frost *et al.* 2000). Terrestriality/arboreality evolved at least five times independently in the Cordylidae (Mouton & Flemming 1999). One can safely assume that the immediate ancestor of the genus *Chamaesaura* was a typical rock-dwelling cordylid with a short, stocky body and well-developed limbs. A reasonable hypothesis would also be that the rock-dwelling ancestor was forced by changes in climate to occupy grass/restioid habitats. A further aim of my study was to determine whether a shift from a rock-dwelling to a grass-living lifestyle posed any constraints for the rock-dwelling ancestor in terms of sheltering options. I selected the Cape girdled lizard, *Cordylus cordylus*, as representative of the ancestral condition.

In summary, my study addressed the following specific questions: (1) During times of inactivity, does *C. anguina* make use of refuge options other than grass and restio tufts? (2) Where does *C. anguina* shelter after a veld fire when the vegetation has largely been destroyed by the fire? (3) Where does *C. anguina* shelter when threatened by fire? (4) As a morphological representative of the rock-dwelling ancestor of *Chamaesaura*, where will *Cordylus cordylus* shelter in a restioid habitat? Both laboratory experiments and field surveys were used to investigate sheltering behaviour in *C. anguina* and to evaluate the impact of fire on this species. Sheltering behaviour in *C. cordylus* was evaluated in the laboratory only.

3.2 MATERIALS AND METHODS

3.2.1 Study animals

The lizards used in this study, were collected at the following localities: Twelve *Chamaesaura anguina* from Landdroskop, Hottentots Holland Mountains, Western Cape, during April 1999; six *C. cordylus* from Gans Bay, Western Cape during April 1999; and six *C. cordylus* from Joostenberg, Western Cape, during September 1999. All lizards were transported to the University of Stellenbosch where they were initially kept in 400 x 600 x 300 mm high glass terraria, supplied with grass tufts in the case of *C. anguina*, and with rocks and crevices in the case of *C. cordylus*. *Chamaesaura anguina* individuals were housed in pairs, while *C. cordylus* individuals were kept in two groups of six. Heat was provided by 40 W spotlights, and water and food (*Tenebrio* larvae) were available *ad libitum*.

3.2.2 Refuge selection in *C. anguina* and *C. cordylus* during times of inactivity

3.2.2.1 Experimental setup: Experiments were conducted in a temperature-controlled room, using six identical glass terraria, 600 x 900 x 500 mm high. The bottom of each terrarium was covered with a 20 cm layer of sand. Ceramic tiles (240 x 120 x 12 mm thick) were used to construct two 'crevices' in opposite corners of all the terraria. Each terrarium was also provided with three 'burrows', made from modified paper cups (80 mm diameter x 95 mm high) buried upside down in the sand layer, in a diagonal line between the two crevices. The cups, with an opening (25 mm diameter) made in the top of each, were lined on the inside with a thin layer of sand. The area between the crevices and burrows was covered with grass tufts. Each terrarium now offered four refuge options namely grass, crevices, burrows and loose sand into which the lizards could wriggle (Figure 3.1). Temperatures were regulated between 28 °C during the day

and 10 °C at night. Light was provided by three sets of four overhead fluorescent tubes, placed in such a way that all terraria received similar light intensities.

3.2.2.2 Trial procedure: The 12 *Chamaesaura anguina* individuals were divided into two groups of six, which were alternately tested. A trial consisted of placing the six lizards of a particular group separately in the six terraria in the temperature-controlled room at 12h00, removing them at 08h00 the following morning, and noting the refuge option that each lizard used during the night. After placing the study animals in the terraria, they were allowed a period of three hours to acclimatize to their new environment. After this, the temperature started to decline from 28 °C to reach a minimum of 10 °C after two hours to ensure lizard inactivity. During the last 30 minutes of the two-hour temperature declining period, the lights were gradually dimmed to simulate dusk and nightfall. The four sets of lights made a gradual decline in light intensity possible by switching off a single set every 10 minutes. This decline in light intensity together with the drop in temperature served as encouragement for the lizards to seek shelter.

3.2.2.3 Refuge selection in *C. anguina*: Two scenarios were created to determine refuge selection of *Chamaesaura anguina* during inactivity.

3.2.2.3.1 Grass tufts present: The lizards were exposed to four refuge options, namely grass, crevices, burrows and loose sand. The refuge choice of each lizard in the six terraria was noted.

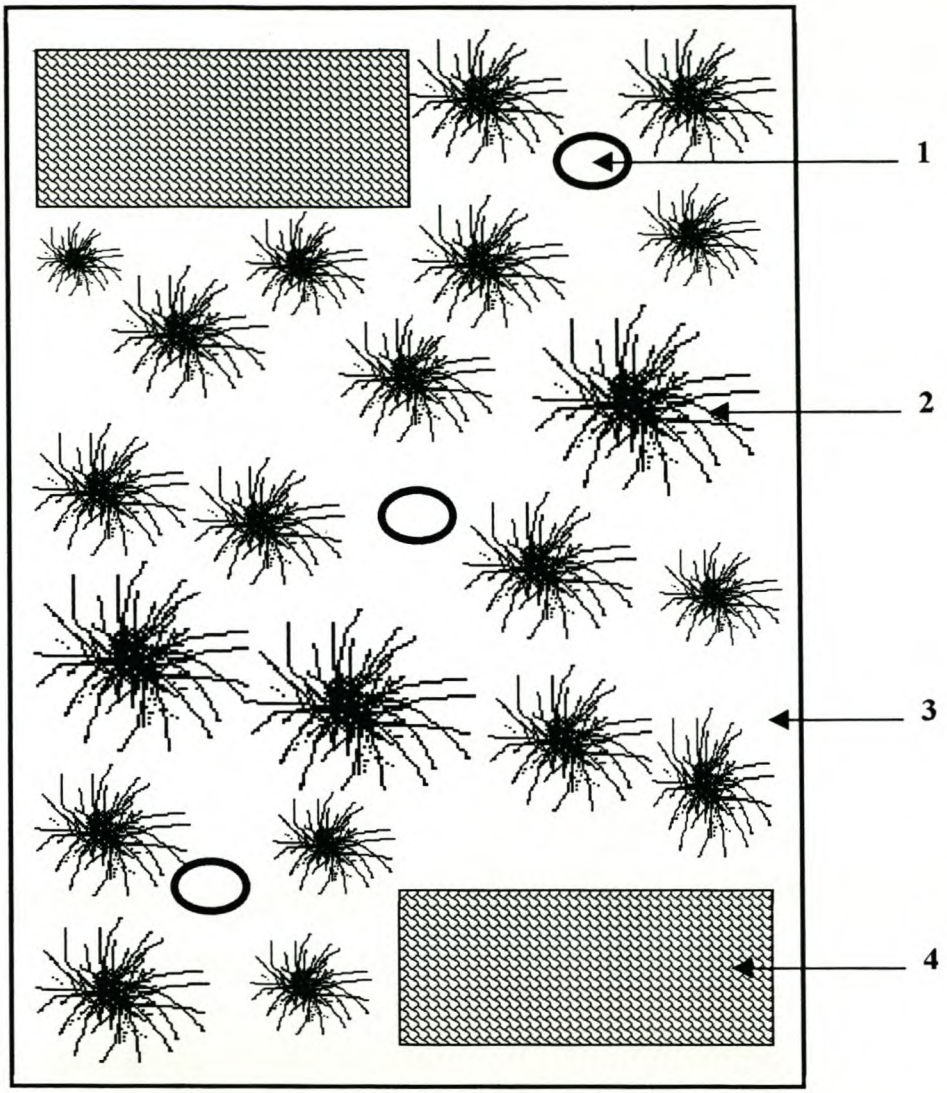

Figure 3.1. Diagram showing the basic lay-out of the four refuge options in a terrarium (900 x 500 x 600 mm) used during experimental trials. 1 - Burrow made from modified foamalite cup; 2 - Grass tuft; 3 – Sand; 4 - Crevice made from ceramic tiles.

3.2.2.3.2 Grass tufts removed: All the grass tufts in the terraria were removed to simulate burnt veld. The lizards were now presented with the remaining refuge options, in contrast to the initial four of the first experiment. The places where the lizards spent their times of inactivity during the night were recorded.

3.2.2.4 Refuge selection in *C. cordylus*: The twelve *Cordylus cordylus* individuals were also divided into two groups of six which were alternatively tested. Two trials were done, one with each group of six lizards. The rock-dwelling *C. cordylus*, in contrast to *C. anguina*, is not dependent on grass for locomotion purposes, and therefore fewer grass tufts were necessary within the terraria for this experiment. The lizards were offered four shelter options namely crevices, grass, burrows and loose sand. As in the previous two experiments, the lizard's choice of refuge was noted the following morning. Only the refuge options that were used by the lizards were taken into account in the statistical analysis of the data.

3.2.3 Refuge selection in *C. anguina* when threatened by fire

3.2.3.1 Experimental setup: This experiment was conducted in a hardboard enclosure (5.4 x 0.9 x 0.9 m) constructed in a well-ventilated shed (Figure 3.2). The floor of the enclosure, covered with a sand-glue mixture, was elevated 0.2 m from the ground. Forty evenly distributed holes (60 mm in diameter) were drilled in the elevated floor of the enclosure. Fifteen of the holes were used to construct 'burrows' by connecting plastic elbow pipes, connected to a brown paper bag at the end of the pipe, underneath the holes in the floor. Grass tufts were placed in the remaining holes within touching distance of one another. Ceramic tiles (240 x 120 x 24 mm thick) were used to construct 15 'crevices', distributed evenly throughout the enclosure. The enclosure now

offered two options, namely crevices and burrows, which could be used to shelter from the fire. The grass tufts provided the necessary substrate for the lizards if they were to flee from the fire. The last meter of the enclosure was covered with only the sand-glue mixture with no surrounding grass tufts, burrows or crevices. This was the section where the lizards, should they flee, would be safe from the heat of the flames. Light was provided by two 500 W spotlights, and food (*Tenebrio* larvae) and water were available *ad libitum*.

3.2.3.2 Trial procedure: A trial consisted of placing four lizards together in an enclosed section (0.7 x 0.9 x 0.9 m) in the enclosure, where they were allowed a 48 hour acclimatization period. Just before each trial, the partition sheets of the enclosed section were removed, allowing them access to the whole enclosure. The dry grass tufts at the side nearest to where the enclosed section was, were set alight (Figure 3.3). A high-speed fan ensured that the grass burned quickly and in the intended direction. The lizards were forced either to seek refuge in the available shelters or to flee from the fire to a safer place. Strict precautions were taken to ensure the survival of all the lizards and to prevent any injuries. At least three people were present during each trial, watching the lizards intently, ready to seize any individual that might be in direct danger. A fire extinguisher and water bottles were always within reach. It was noted whether the lizards made use of the refuge options, or whether they fled. The experiment was repeated three times, each trial with a different set of four specimens. At the end of each trial the burnt grass tufts and ashes were removed. The enclosure was cleaned and provided with fresh tufts.

Figure 3.2. The enclosure (5.4 x 0.9 x 0.9 m) used in the fire experiment, provided with grass tufts, "burrows" and "crevices".

Figure 3.3. The grass tufts were set alight at one end of the enclosure.

3.2.4 Data analysis

Statistical analyses of the data included the comparison of an expected outcome with the actual outcome, using the Chi-square test or the Fisher Exact test (in the case of smaller data sets with only two options) to determine whether a significant difference ($P < 0.05$) between the two outcomes existed. The expected statistical outcome predicted that the lizards would equally prefer the different options. During periods of inactivity the lizards had to choose between the different refuge options. When threatened by fire, the lizards had two options, namely to flee or not to flee and rather use the shelters.

3.2.5 Case studies

Case studies regarding *Chamaesaura anguina* sightings during and after veld fires at different locations were described. From the beginning of 1999 until late 2000 most mountain fires in the Western Cape Province were monitored. All burnt mountain sites in this region that might be of some relevance to this study were visited within a few days after the fire, and information about the fire was gathered from the rangers of that area. Where possible, burnt areas were searched for dead or live *C. anguina* lizards.

3.3 RESULTS

3.3.1 Refuge selection during times of inactivity

3.3.1.1 Refuge selection in *C. anguina*

3.3.1.1.1 Grass tufts present: The null-hypothesis stated that the lizards would equally prefer the four different refuge options. A significant difference was found between the expected and actual outcomes (Chi-square = 12.00; $df = 2$; $P < 0.05$). All 12 lizards chose the grass tufts as refuge option rather than making use of the crevices or burrows

as shelter sites during the night. The study animals were either positioned coiled-up horizontally within the grass tuft, or were lying in the tuft in an outstretched fashion.

3.3.1.1.2 Grass tufts removed: In the second experiment, when the grass tufts were removed, the expected outcome predicted that four lizards would shelter in the crevices, four would use the burrows, and four would not make use of the shelters. There was a significant difference between the expected and the actual outcomes (Chi-square = 6.17, $df = 2$; $P < 0.05$). Two of the 12 lizards were found sheltering in the refuges, one in a crevice and one in a burrow. The 10 remaining lizards were found lying on the sand in the terraria, not making use of the optional shelter sites during the night.

3.3.1.2 Refuge selection in *C. cordylus*: Only two refuge options were equally utilized by *Cordylus cordylus*, namely the crevices and grass tufts. No significant difference existed between the expected and actual outcomes for the utilization of these two shelter options (Fisher-exact; P = 1.00). When the lizards were hiding in the grass tufts, they were usually hiding in the dense bottom part of the tuft, sometimes positioned upside down, clinging to the grass.

3.3.2 Refuge selection in *C. anguina* when threatened by fire

The expected outcome predicted that four lizards would use the crevices, four the burrows, and four would not make use of the refuges. A statistical significant difference existed between the outcome that was expected from random occurrence and the actual outcome (Chi-square = 6.17, $df = 2$; $P < 0.05$). Two lizards sought refuge in the shelters provided, one in a crevice and one in a burrow. Of the remaining 10 lizards, six fled from the approaching flames until they reached the end section of the enclosure that

lacked grass tufts, burrows or crevices. The other four were trapped by the flames when they tried to flee or hide in the grass tufts and would have burnt to death had we not intervened.

3.3.3 Case studies

I. Swartberg Pass, Western Cape Province, 1985 (P.le F.N. Mouton, personal communication): Mouton was driving along the Swartberg Pass road while a fire was raging in fynbos vegetation beside the road. He saw several *Chamaesaura anguina* individuals falling down the road cutting onto the road. He counted at least 10 individuals stranded on the road along a short section of ± 500 m where the fire burnt right above the road.

II. Boosmansbos, Langeberg Mountains, Western Cape Province, 1987 (P.le F.N. Mouton, personal communication): Within days after a fire destroyed a large section of the Boosmansbos Wilderness Area in the Langeberg Mountains, Mouton was part of a hiking group that visited the area. In an area where the fire burnt right down to the jeep track along which they walked, they found 14 *C. anguina* individuals stranded in vegetation in a shallow furrow along the mountainside of the track. The lizards did not attempt to flee when they collected them.

III. Landdroskop, Hottentots Holland Mountains, Western Cape Province, 1999 (personal observations): An extensive mountain fire during March that year swept an area of 45 000 ha in these mountains. One week after the fire, a party of four visited the Landdroskop locality to assess the impact of the fire on the local *C. anguina* population. Two persons searched along a footpath on the northern slope of Landdroskop, while the other two systematically searched a

large section of the burnt area for live or dead grass lizards. A special attempt was made to look underneath as many rocks as possible. All unburnt vegetation patches were also searched. Ten individuals were collected in a few unburnt restio tufts along the footpath, which, being well-cut into the mountain side, provided some protection for both vegetation and lizards (Figure 3.4). No dead grass lizards were recorded along the path, but a single dead *Cordylus oelofseni* (rock-dwelling cordylid) was found. Six more individuals were found along a short section of a jeep track that was surveyed. Like the footpath, the track was at places well-cut into the mountain side and also had a shallow drainage furrow on the same side which provided protection for both vegetation and grass-lizards. All six lizards were found sheltering in isolated restio tufts that survived the fire. A three hour search of a large burnt area, where grass lizards were recorded before the fire, yielded no lizards, either dead or alive. Five days after the first visit to Landdroskop, the locality was visited again and that, 14 *C. anguina* individuals were observed hiding in the remaining unburnt grass tufts in the ditch next to the road along a 500 m section. Two months later, only six individuals were found in the same 500 m section. Three months after that, eight individuals were observed, of which six were juveniles and two adults, in the tufts next to the road, as well as in one of the restio "islands".

IV. Groenlandberg, Hottentots Holland Mountains, Western Cape Province, 1999 (L. Lourens, personal communication, observation): During a fire that swept this part of the mountains, birds, especially crows, caught *C. anguina* lizards that fled in front of the fire. The birds also ate the already burnt individuals that lay in the ashes. Many *C. anguina* lizards tried to find refuge in the gravel roads, but most of them were also caught by birds or were run over by motor cars. In

one 20 m section a ranger counted five dead *C. anguina* individuals. Two days after the fire we walked a 4 km transect through the burnt habitat, but found no dead or live lizards.

V. Kogelberg Nature Reserve, Western Cape Province, 2000 (personal observation): Two months after a veld fire that occurred in January, two *C. anguina* lizards were found hiding in unburnt grass tufts next to a footpath in the reserve. These tufts were the only unburnt vegetation in the whole burnt area. No dead individuals were found.

VI. Grootwinterhoek Mountains, Western Cape Province, 2000 (K. de Bruin, personal communication, observation): De Bruin claims that during a mountain fire in this area he saw *C. anguina* lizards fleeing from the flames. Predators like birds made use of this situation by preying on the fleeing lizards. One week after that, no lizards were found in the burnt habitat, and no individuals were found hiding in the tufts next to the burnt veld.

VII. Montagu Pass, George, Western Cape Province, 2000 (personal observation): A mountain fire started at the top of the mountain in late September, burning down towards the road where it was extinguished. The next day 11 *C. anguina* lizards, of which 8 were females, were collected along a 200 m section of the road. They were sheltering in the only remaining grass tufts, that occurred in a shallow drainage furrow, on the mountain side of the road (Figure 3.5). None of the lizards attempted to flee when they were collected. A part of a body of a grass lizard was also found that clearly had been killed by a predator. Also in the grass tufts were found two *Tropidosaura gularis* and one *Mabuya homalocephala*. No dead or live *C. anguina* lizards were found amongst the ashes or underneath rocks in the burnt area.

Figure 3.4. A footpath at Landdroskop in the Hottentot Holland Mountains which provided some protection from the fire for both vegetation and *Chamaesaura anguina* lizards.

Figure 3.5. A shallow drainage furrow on the mountain side of the road at Montagu Pass, George, which provided some protection from the flames for both the vegetation and *Chamaesaura anguina* lizards.

3.4 DISCUSSION

3.4.1 Refuge selection in *C. anguina*

Results of experiments conducted in this study, as well as available field data, clearly indicate that the Cape Grass lizard, *Chamaesaura anguina*, seldom makes use of shelter options other than grass and restio tufts, even when threatened by fire. In the case of fire, it flees from the fire by so-called 'grass-swimming', a form of lateral undulatory movement (see Gans 1975). Field observations also suggest that mortality during fire is considerably higher than in the case of rock-dwelling cordylids and non-elongated terrestrial lizards.

One of the most critical aspects of any animal's life is its escape and sheltering behaviour (Losos & Irschick 1996). Most limbless squamates, excluding snakes, are either fossorial, use burrows, or shelter under objects on the ground (Gans 1975; Garland & Losos 1994). From field observations, it is clear that *C. anguina* relies heavily on crypsis and immobility, but only to a certain point, after which it resorts to flight. When remaining motionless in the grass or restioid habitat, these lizards are virtually impossible to see, even at a short distance. Should one, however, venture too close, they will flee at great speed by grass-swimming for distances up to 30 m, where they will 'freeze' again. It is clear that fleeing by grass-swimming is an integral part of the escape strategy when threatened by either predators or fire. Predation and fire thus could have acted as key environmental pressures in the evolution of extreme body elongation and limb reduction in this clade to facilitate lateral undulatory movement.

Predator escape strategies, foraging strategies, and habitat specificity more often than not are co-evolved phenomena, all able to influence the morphology of a species (Vitt & Price 1982). *Chamaesaura anguina*, like other cordylids, follows a sit-and-wait foraging strategy (unpublished data). In general, sit-and-wait foragers rely on crypsis

rather than speed as a predator avoidance mechanism (Vitt & Congdon 1978; Vitt & Price 1982). Grass-lizards of the genus *Chamaesaura* appear to be an exception to this rule in that both crypsis and speed are equally important in predator avoidance strategies. Sit-and-wait foragers normally need a good field of view in order to locate prey. In the restioid and grassland habitats, this requires positioning of the lizard on top of the vegetation. In *C. anguina*, this is achieved by the elongated body which allows for sufficient weight distribution. Similar to the way in which a chamaeleon uses its tongue to catch prey, the elongated body of grass lizards also allows prey to be captured across open spaces in the vegetation. Clearly, foraging dynamics also played a major role in the evolution of body elongation in this clade.

Fynbos and grassland, which form the main habitat for grass lizards in southern Africa, are fire-prone vegetation types. In fact, fynbos is considered a pyrophylic (fire loving) vegetation, dominated by plants with life strategies tuned to the fire regime (Deacon *et al.* 1992). *Chamaesaura anguina* is mainly associated with two fynbos communities, restioid fynbos and grassy fynbos. Restioid fynbos is characterised by the predominance of restioids and the poor cover or total absence of shrubs, particularly tall ones (Cowling & Richardson 1995) and is characteristic of the western part of the fynbos region. In the eastern part, the restioids are replaced by summer-growing subtropical grasses to form the grassy fynbos community (Cowling & Richardson *op cit.*). The key components of a fire regime are the frequency, seasonality, and intensity of fires (Gill 1975). Fire recurrence intervals and seasonality are relatively predictable (Van Wilgen 1984, Johnson & Van Wagner 1985), but fire intensity depends primarily on fuel moisture, air temperature and wind speed (Cheney 1981; Van Wilgen *et al.* 1985), all relatively unpredictable factors. Restioid fynbos is most likely to burn in summer, grassy fynbos in spring and autumn, and grassland in winter (Le Maitre &

Midgley 1992). On average, most fynbos plant communities burn every 12 to 15 years (Cowling & Richardson 1995). In grassy fynbos in the eastern regions, where fuel accumulates more rapidly owing to the fast growth of summer-active grasses, fire frequency is, on average, higher than in the west, ranging between four and six years (Cowling & Richardson 1995). Fire cycles of less than four years are seldom possible in fynbos communities (Van Wilgen *et al.* 1992). Lightning is the primary natural source of ignition for fynbos fires and increases in frequency from 0.2 in the west to 3.4 ground strikes per square kilometer per year inland and in the east (Edwards 1984).

It is clear that fire regimes differ from east to west in southern Africa and that the impact of fire on *C. anguina* may be different in different parts of its range. The general minimum period of four years of recovery required by most fynbos communities before being able to burn again, is ecologically important for the survival of grass lizards in any area. Recurrence times of less than four years would probably not allow sufficient time for recruitment and grass lizards would become locally extinct.

Although fire intensity has a big influence on survival rates, direct mortality of lizards caught in veld fires has generally been assumed to be low (Means & Campbell 1981; Bamford 1995; Griffiths & Christian 1996). By sheltering in trees or hollow termite mounds, the arboreal frillneck lizard (*Chlamysosaurus kingii*) from the Australian woodlands, is hardly affected by low intensity fires, (Griffiths & Christian 1996). Fyfe (1980) found a relatively high fire survivorship for most of the species that he studied that retreat underground when threatened. E.H.W. Baard (personal communication), in the controlled burning of Swartboskloof in the Hottentots Holland Mountains by Cape Nature Conservation authorities, found that numbers of rock agama, *Agama atra*, and red-sided skink, *Mabuya homalocephala*, were in fact higher after the

fire than before. Although this anomaly must be attributed to increased visibility after the fire, it also suggests that the impact of the fire on these two species was minimal.

Although data on dynamics of *Chamaesaura* populations before and after fire, are lacking, and probably always will be because of the extreme difficulty of locating these lizards in the wild, anecdotal data suggest that fire has a considerable impact on this species, several orders of magnitude greater than on rock-dwelling or non-elongated terrestrial lizards occurring in the same area. Data suggest that not only is direct mortality during the fire high, but also mortality among survivors after the fire, owing to increased exposure to predators, food shortages, and thermoregulatory constraints. The susceptibility of grass lizards to veld fires is highlighted by observations made on *Chamaesaura macrolepis* by Bruton (in Boycott 1990), who recorded 122 dead lizards during burning of firebreaks in grassland areas in Maputaland. Boycott (1990) reported that in 1988, a day after a wild fire entered the Malolotja Nature Reserve in the highveld region of Swaziland, where much of the grassland is burned annually for stock grazing, five dead *C. anguina* individuals were found along a 2 km section.

A decline in insect abundance, especially grass eating invertebrates, usually follows a veld fire (Nagel 1973; Warren *et al.* 1987; Collins & Gibson 1991; Cavitt 2000). *Chamaesaura anguina* individuals that survive a fire, will certainly in many cases have to cope with food shortages, especially those individuals that are stranded in a single restio or grass tuft. Capturing of prey may also be significantly more difficult in the absence of suitable vegetation because locomotion is impeded. Five individuals that we found stranded in isolated restio tufts three weeks after a fire, had completely empty stomachs. Removal of vegetation and litter layer by fire may result in serious thermoregulatory problems for surviving lizards due to increased exposure to temperature fluctuations (Hulbert 1969; Rice & Parenti 1978; Fyfe 1980; Cavitt 2000).

Chamaesaura anguina individuals surviving a fire may be extremely exposed in that this species does not seem to utilize any sheltering option other than grass and restio tufts.

High mortality due to veld fires is not restricted to grass lizards (Wright 1988). During January 2000 about 90 % of an angulate tortoise population (*Chersina angulata*), occurring in the West Coast National Park in South Africa, died in an extensive veld fire (Baard 2000). Tortoises being oviparous and laying several clutches throughout the year, many tortoise eggs are expected to have survived the fire and recruitment may be relatively quick. In the case of grass lizards, one would also expect certain adaptations to facilitate recruitment after a major fire. It comes as no surprise that fecundity in *C. anguina* is more than four times that in other cordylids (see Chapter 4). In a family where the female reproductive cycle is very conservative and strongly seasonal, it is also noteworthy that the female cycle of *C. anguina* is completely aseasonal, in other words that individual female cycles are not synchronised (see Chapter 4). No matter what time of the year a fire may occur, there are bound to be some pregnant females among the survivors.

3.4.2 Refuge selection in *C. cordylus*

The results of my study show that the rock-dwelling species, *Cordylus cordylus*, had no problem sheltering in grass tufts. As a morphological representative of the ancestor of grass lizards, this suggests that the historical shift from rock-dwelling to grass-living lifestyles did not pose any serious problems in terms of refuge selection. Foraging and thermoregulation, on the other hand, might have presented more serious problems. In fact, I believe that foraging and thermoregulatory pressures were the main causes of body elongation and limb reduction in the ancestor of grass lizards. For effective

feeding and thermoregulation, it would have been necessary for the lizard to position itself on top of the grass /restios, firstly for a clear view of the environment to spot potential prey, and secondly, to obtain direct sunlight. As mentioned before, to achieve this, an elongated body would have been necessary for sufficient weight distribution. Continued body elongation would eventually have restricted refuge possibilities in the grass/restio habitat and escape behaviour by grass-swimming would slowly have evolved, adding further pressure for body and tail elongation.

3.4.3 Summary and conclusions

Chamaesaura anguina does not shelter underneath rocks or in burrows and is accordingly highly susceptible to fire. Fleeing by undulatory locomotion might be their only survival option and might have been an important driving force in the evolution of body elongation and limb reduction. Direct mortality due to fire is normally high and survivors may face increased predation, food shortages and thermal exposure. Recruitment is facilitated by high fecundity and aseasonal reproduction. *Cordylus cordylus*, had no problem sheltering in grass tufts and as a morphological representative of the ancestor of grass lizards, this suggests that the historical shift from rock-dwelling to grass-living lifestyles did not pose any serious problems in terms of refuge selection. For effective feeding and thermoregulation, an elongated body would have been necessary for sufficient weight distribution in the grass/restio habitat. Continued body elongation would have restricted refuge possibilities in the grass/restio habitat and escape behaviour by grass-swimming would slowly have evolved.

CHAPTER FOUR

REPRODUCTION AND SEXUAL DIMORPHISM IN THE CAPE GRASS LIZARD, *CHAMAESAURA ANGUINA*

4.1 INTRODUCTION

Reproductive cycles of most lizards are usually closely correlated with climatic factors, including photoperiod, temperature and rainfall (Fitch 1970; Duvall *et al.* 1982; Licht 1984). Most temperate zone forms are strictly seasonal with well-defined periods of activity followed by periods of quiescence (Fitch 1970; Duvall *et al.* 1982; Licht 1984). Tropical species, on the other hand, are either seasonal breeders, dependent on food availability and rainfall, or aseasonal ones, where reproductive activity is a year round phenomenon (Fitch 1970, 1987; Licht 1984; Guillette & Mendez-de la Cruz 1993; Mouton & Herselman 1994). Previous studies on reproductive cycles of members of the Cordylidae have shown that females of all species exhibit the same basic pattern of autumn/winter vitellogenic activity, with winter/spring ovulation and gestation in the following late summer to autumn (Van Wyk 1989, 1991; Flemming 1993a; Van Wyk & Mouton 1996, 1998). Guillette & Mendez-de la Cruz (1993) and Mendez-de la Cruz *et al.* (1998) suggested that autumn/winter reproductive activity might be associated with the evolution of viviparity in certain squamate genera.

Testicular cycles in cordylid lizards conform to two basic types (Van Wyk 1990; Flemming 1993b; Van Wyk 1995; Van Wyk & Mouton 1996, 1998). In those species displaying a pre-nuptial cycle, spermiogenic activity takes place during late autumn through spring, thereby immediately preceding mating (Van Wyk 1995; Van Wyk & Mouton 1998). Testicular regression sets in during summer, making sperm storage

unnecessary (Van Wyk 1995; Van Wyk & Mouton 1998). Male and female gonadal cycles are generally well synchronized (Van Wyk 1990; Flemming 1993b; Van Wyk & Mouton 1996). In cordylids that display a post-nuptial cycle, testes are regressed during spring and summer when mating and gestation are evident (Van Wyk 1995; Van Wyk & Mouton 1998). Spermatogenesis starts in summer with spermiogenesis reaching a peak in autumn (Van Wyk 1995; Van Wyk & Mouton 1998). Sperm is stored in the epididymis and vas deferens after testicular regression in late autumn and winter until mating occurs in spring (Van Wyk 1995; Van Wyk & Mouton 1998). In species displaying this type of cycle, male and female gonadal activity is regarded as asynchronous (Van Wyk 1995). Pre-nuptial spermatogenesis is usually exhibited in temperate zone lizards, whereas post-nuptial spermatogenesis is common among temperate zone snakes and chelonians (Bradshaw 1986; Jameson 1988; Van Wyk 1995).

Information regarding reproductive cycles and sexual dimorphism in members of the genus *Chamaesaura* is limited to general comments in the literature. *Chamaesaura* species differ markedly in morphology from the other cordylids by displaying extreme diametric reduction, body/tail elongation and limb reduction (Branch 1998; Mouton & Flemming 1999). This study firstly examines the male and female reproductive cycles of the Cape grass lizard, *Chamaesaura anguina*. Bearing in mind the susceptibility to fire of this species, one could expect certain adaptations regarding timing of reproductive events and fecundity, to facilitate successful recruitment after a fire. In addition, if more cordylid males following a post nuptial reproductive cycle can be examined, a clearer picture concerning the evolution of this cycle, may emerge. Information regarding sexual size dimorphism (SSD) could be a relevant indication of female fecundity, and was accordingly the second objective of

this study. Female-biased SSD has, to date, been recorded for only three cordylid species, while all the other cordylids for which data are available, are rock-dwelling forms with either male-biased SSD or with sexes being of equal size (Mouton & Van Wyk 1993; Mouton *et al.* 2000). All three *Chamaesaura* species are viviparous and occur in escarpment and montane grasslands, with *C. anguina* occurring along the southern and eastern coastal regions of South Africa (Lang 1991; Mouton & Van Wyk 1997).

4.2 MATERIALS AND METHODS

4.2.1 Specimen collection and study area

I examined specimens of the Cape grass lizard, *Chamaesaura anguina*, in the Ellerman collection (Department of Zoology, University of Stellenbosch), as well as in the collections of the South African, the Port Elizabeth, and Transvaal Museums. I also collected additional specimens from several localities along the Cape Fold Mountains in the Western Cape. Specimens were sacrificed within 36 hours after capture and preserved in 70 % ethanol.

The Western Cape is characterized by a high annual rainfall occurring mostly in the winter with a dry summer period (Schultze & McGee 1978). Climatological data were obtained from three weather stations in the Cape Fold Mountain region and surrounding area: Slanghoek Kelders, 3339S/1914E (880m); Jonkershoek, 3358S/1856E (244m); Vergelegendruif, 3403S/1855E (85m). Average monthly rainfall, as well as average monthly air temperatures for the years 1997 - 1999 are shown in Figure 4.1.

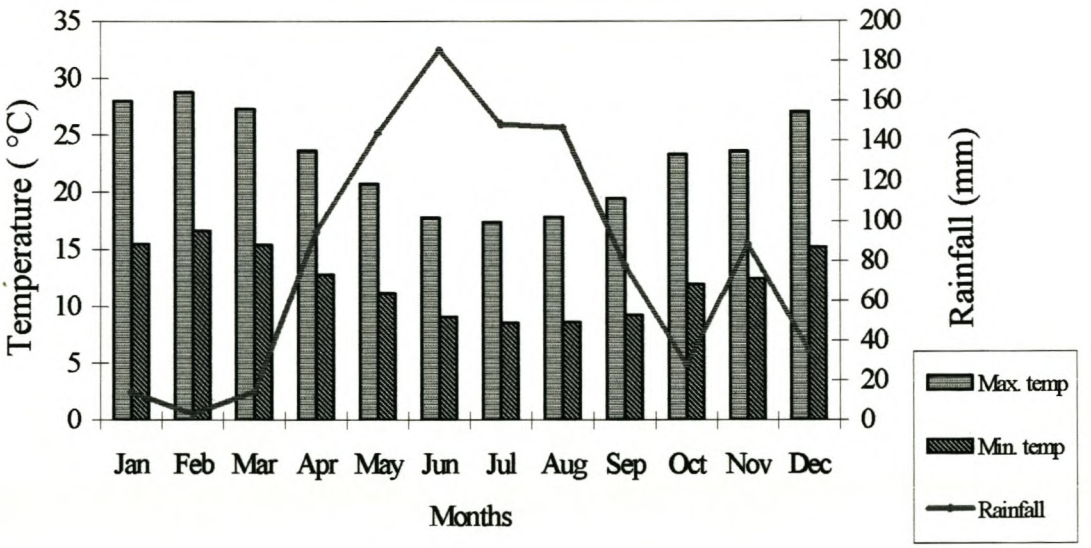

FIGURE 4.1. Average maximum ambient temperatures, average minimum ambient temperatures, and total monthly rainfall for the years 1997 - 1999 recorded in and around the Hottentots Holland Mountain area.

4.2.2 Female reproductive cycle

Eighty-five females were available for inspection. The reproductive status of adult females was determined on the basis of the appearance of ovarian follicles, and the presence or absence of oviductal eggs. Females were grouped into four reproductive categories: pre-vitellogenic, early vitellogenic, pre-ovulatory and gravid (Van Wyk & Mouton 1998). Both ovaries were examined and the diameters of two or three of the largest follicles in each ovary were measured to the nearest 0.01 mm, using a stereomicroscope. Oviductal eggs were counted only and not measured. Follicles smaller than 3.0 mm were considered pre-vitellogenic, and follicles with diameters between 3.0 mm and 5.0 mm as early vitellogenic. Females having vitellogenic follicles larger than 5.0 mm, were considered pre-ovulatory, and those having oviductal eggs or embryos as gravid.

4.2.3 Male reproductive cycle

Forty-six males were available for examination. For each male, the longest and shortest axes of the right testis were measured to the nearest 0.01 mm with a digital caliper under a stereomicroscope. Testicular volume was calculated, using the formula for an ellipsoid ($V = 4/3\ \pi\ a^2b$, where a = ½ x shortest diameter and b = largest diameter) (Mayhew 1963). The right testis, as well as part of the ductus epididymis, was removed, dehydrated in ethanol, cleared in xylene, embedded in paraffin, sectioned at 8 - 10 μm, and stained with Erlich's hematoxylin and eosin (Humason 1967). The image of each sectioned testis was digitilized, and a total of 10 seminiferous tubule diameters were measured, using the LIDA software package (Leica). Spermatogenic activity was assessed qualitatively using Licht's (1967) classification system. Eight stages were recognized (Table 4.1), where Stage 8 represented complete regression (Mayhew 1971;

Van Wyk 1995). Presence of spermatozoa in the epididymis was examined, and males were considered sexually mature if spermatozoa were present either in testes or epididymes.

Data were subjected to the Kolmogorov-Smirnov normality test and Levene's test for homogeneity of variances, respectively, before statistical analyses were performed (Sokal & Rohlf 1981). Analyses of variance (ANOVA) were used to establish whether or not significant variation in testis volume and seminiferous tubule diameter among months existed. The relationship between testis volume and seminiferous tube diameters, as well as between testis volume and SVL, was examined using Pearson's correlation test. In all analyses, differences were considered significant at $P < 0.05$. Statistical procedures were performed using the STATISTICA, '99 edition, software package (StatSoft).

4.2.4 Sexual dimorphism and clutch size

Snout-vent length (SVL) of 144 specimens was measured to the nearest 0.01 mm using digital callipers. Sexual size dimorphism (SSD) recorded for *Chamaesaura anguina* was quantified by a size dimorphism index (SDI), following Mouton *et al.* (1999):

$$\frac{\text{mean SVL of adults of female sex}}{\text{mean SVL of adults of male sex}}$$

with the result being defined as positive when females were larger, and negative when males were larger (Gibbons & Lovich 1990; Mouton *et al.* 1999). Furthermore, a maximum size dimorphism index (SDImax) based on the mean SVL of the largest 25 % of each sex, was calculated. Data were subjected to the Kolmogorov-Smirnov

normality test and Levene's homogeneity test. In the case of abnormally distributed data, the Mann-Whitney U-test was used for comparing two means. Differences were considered significant at $P < 0.05$. The relationship between SVL and clutch size of the gravid females was examined using Pearson's correlation analysis.

4.3 RESULTS

4.3.1 Female reproductive cycle

The smallest gravid *Chamaesaura anguina* female measured 89.10 mm SVL. Therefore, only females with similar or larger SVL's were considered as adults. Sixteen females in the sample were considered to be juveniles. Seasonal variation in reproductive stage among *C. anguina* females (N = 69) is presented in Figure 4.2. Unfortunately, owing to the extreme difficulty of collecting these lizards and low numbers in museum collections, I was able to examine only a few representatives for most of the months. During the month of June (N = 12) all four reproductive stages were recorded among the females examined. Gravid females, with embryos in different stages of development, were collected during all the months, except April (N = 2), August (N = 1) and December (N = 1). For the specimens from the Western Cape, no apparent correlation existed between climatological changes (Figure 4.1) and the timing of reproductive events (Figure 4.2).

4.3.2 Male reproductive cycle

The smallest reproductively active (i.e. spermatozoa present in testes or epididymis) *Chamaesaura anguina* male was collected during September and measured 75.36 mm SVL. It had a testis volume of 8.45 mm^3. Testis volume (ANOVA; $F_{(7,22)} = 3.70$; $P < 0.05$; Figure 4.3), as well as seminiferous tube diameter (ANOVA; $F_{(10,25)} = 4.895$; $P <$

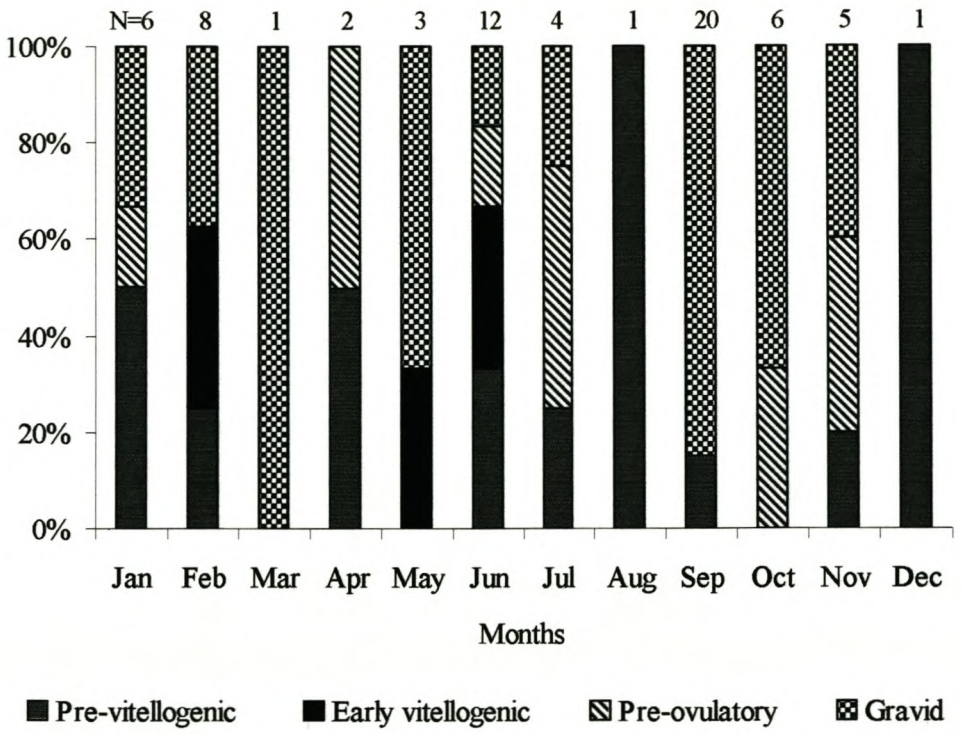

FIGURE 4.2. Stacked bar diagram showing the percentages of *Chamaesaura anguina* females in the various reproductive stages throughout the year.

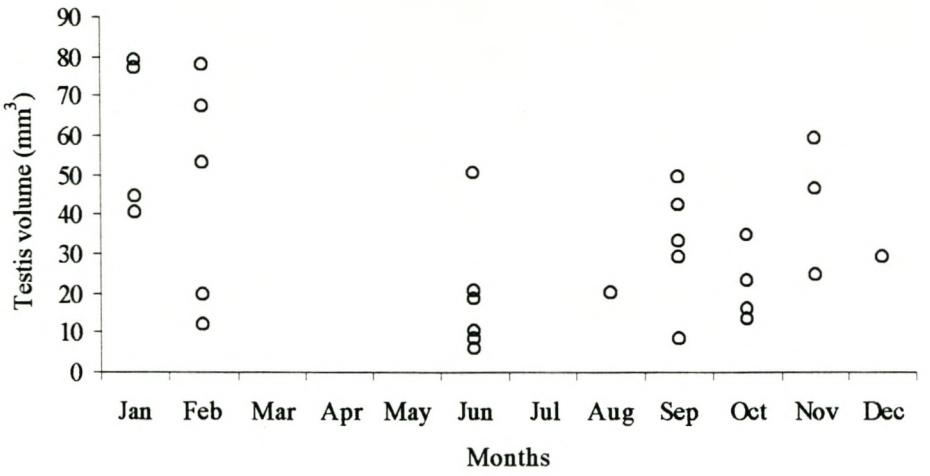

FIGURE 4.3. Scatterplot of testicular volume against months of the year for *Chamaesaura anguina* males.

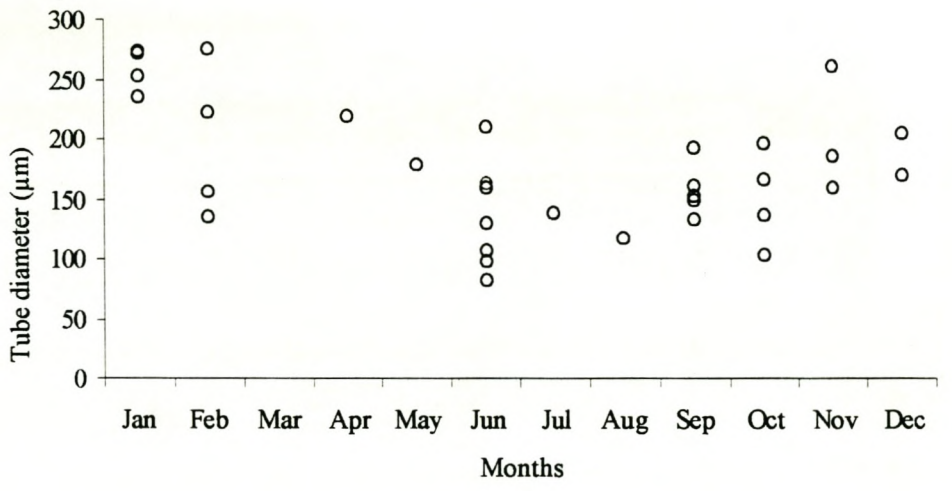

FIGURE 4.4. Scatterplot of seminiferous tube diameter against months of the year for *Chamaesaura anguina* males.

TABLE 4.1. Seasonal changes in male spermatogenic activity in the lizard *Chamaesaura anguina*. Classification of spermatogenic stages was adapted from Licht (1967), Mayhew (1971) and Van Wyk (1995): (1) Seminiferous tubules involuted with spermatogonia only; (2) Primary spermatocytes appearing; (3) Secondary spermatocytes and early spermatids appearing to abundant; (4) Transforming spermatids with few spermatozoa; (5) Spermatids and spermatozoa abundant; (6) Spermatozoa abundant (maximal level of spermiogenesis); (7) Spermatozoa abundant, but spermatids and spermatocytes greatly reduced; (8) Involuted with only spermatogonia, many spermatozoa.

		Spermatogenic stages with number of lizards in each stage							
Month	**N**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Jan	4					2	2		
Feb	5					1		2	2
Mar	0								
Apr	1			1					
May	2		2						
Jun	8		4	4					
Jul	1		1						
Aug	1		1						
Sep	6		4	2					
Oct	4		2	2					
Nov	3			1	1		1		
Dec	2							2	

0.05; Figure 4.4) varied significantly throughout the different months. Histological examination indicated that testes were in a regressed state during April through to October (Stages 1-3; Table 4.1). Spermiogenic activity started in spring with the seminiferous tubules containing a few spermatozoa (Stage 4; Table 4.1). Spermiogenesis was at its peak during late summer with spermatozoa abundant in the seminiferous tubules (Stages 5-8; Table 4.1). The correlation between testis volume and seminiferous tubule diameter was positive and significant ($r = 0.89$; $P < 0.05$), while no significant correlation existed between testis volume and SVL ($r = 0.41$; $P > 0.05$). Spermatozoa were present in lumina of epididymi and vasa deferentia from January through to early October, but only one individual of three in September, and one of three in October. Onset of spermatogenesis during late spring/early summer of males from the Western Cape, coincided with increasing ambient temperatures and decreasing monthly rainfall (Figure 4.1).

4.3.3 Sexual dimorphism and clutch size

The arrangement of body size classes indicated that females reach larger sizes than males (Figure 4.5). Females in the sample ($N = 91$) ranged in size from 55.68 mm to 152.50 mm, while the males ($N = 53$) ranged from 63.38 mm to 115.12 mm. The mean SVL of females (109.51 mm ± 20.60 SD) was significantly larger (Mann-Whitney; $P < 0.001$) than that of males (84.77 mm ± 9.39 SD). A significant difference (Mann-Whitney; $P < 0.001$) was also found between mean SVL of the upper 25 % of the sample of each sex, with a mean of 134.22 mm ± 9.45 SD ($N = 23$) for adult females and a mean of 95.89 mm ± 6.81 SD ($N = 13$) for adult males. A positive SDI of 1.29 and a SDImax of 1.40 were calculated. Clutch size, determined from 34 gravid females,

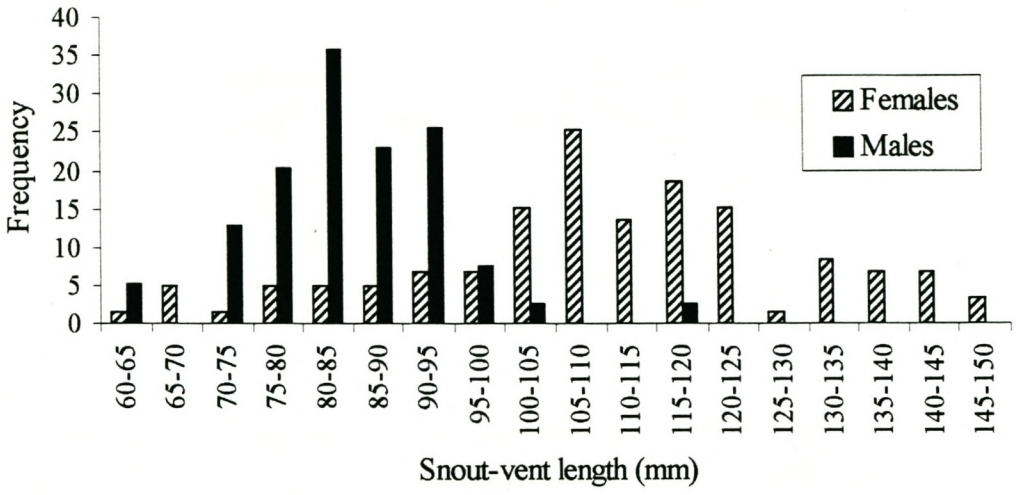

FIGURE 4.5. Frequency histogram of body size distributions for female and male *Chamaesaura anguina*.

varied from 3 - 17 (6.41 ± 2.97). A positive correlation existed between clutch size and female SVL ($r = 0.69$; $P < 0.05$).

4.4 DISCUSSION

4.4.1 Female reproductive cycle

Females of all cordylid species for which detailed reproductive data are available, namely *Cordylus giganteus* (Van Wyk 1991, 1994), *C. polyzonus* (Van Wyk 1989; Flemming & Van Wyk 1992), *Pseudocordylus melanotus* (Flemming 1993a), *P. capensis* (Van Wyk & Mouton 1998), *Platysaurus capensis* and *P. minor* (Van Wyk & Mouton 1996), display strictly seasonal reproductive cycles. They exhibit autumn/winter vitellogenesis, with the timing of reproductive events among females of each species well synchronized (Van Wyk & Mouton 1996, 1998). The onset of vitellogenesis in *Chamaesaura anguina* females, unlike other Cordylidae lizards, does not match the pattern of autumn/winter vitellogenic activity. This study shows that reproductive events are poorly synchronized among *C. anguina* females. From most studies regarding autumn/winter reproductive cycles, it is apparent that female cycles are normally relatively conservative, and therefore under phylogenetic constraint (Guillette & Mendez-de la Cruz 1993; Van Wyk & Mouton 1998). However, in instances where intraspecific variation concerning the onset of vitellogenesis, ovulation, and parturition between the females does occur, it may be considered phenotypic responses to different environmental conditions, rather than genetically-based characters (Dunham *et al.* 1988; Flemming & Van Wyk 1992).

There are two possible explanations for the reproductive pattern observed in *C. anguina*. Firstly, the possibility exists that *C. anguina* females follow a seasonal reproductive cycle, much like that of other cordylids, but that this cycle is easily

disrupted by environmental factors, resulting in intraspecific variation in reproductive events. Thirty percent of the females in the sample deviated from the cordylid autumn/winter vitellogenic cycle (Figure 4.2). It is highly unlikely that there would be so many outliers only by chance. Only one out of ten females collected at Montagu Pass, for example, were not in the same reproductive phase as the other females. Environmental control, at least in this species, may thus be more complex than initially expected. Ambient temperature has been implicated as one of the primary factors regulating growth rates and the onset of reproductive activity in reptiles, probably by determining the amount of time that is available for feeding and growth (Dunham *et al.* 1988; Flemming & Van Wyk 1992). Except for ambient temperature, other factors such as photoperiod and moisture may also have a profound influence and may not be overlooked (Duval *et al.* 1982; Licht 1984; Flemming & Van Wyk 1992). If such environmental factors were the cause of reproductive pattern disruption in *C. anguina*, then one would have expected reproductive events of females from the same locality to be synchronized. This is, however, not true for *C. anguina* females, because females from the same locality were often out of phase.

Habitat destruction caused by veld fires may lead to variation in certain environmental factors, which in turn might influence reproductive events of *C. anguina*. Veld fires are a frequent phenomenon in the southern African grasslands and fynbos areas, and on average 3 - 6 major fires per year are caused by lightning alone in the Western Cape Boland District (M. Gentle, personal communication). Environmental factors like strong, frequent winds together with hot, dry summers play a tremendous role in promoting the occurrence of veld fires in this area (M. Gentle, personal communication; Cowling & Richardson 1995). Grassland habitat specificity makes *C. anguina* susceptible to veld fires and habitat destruction (see Chapter 3). Some lizards

that manage to survive fires are often restricted to 'grass islands' or single grass tufts where the sparsely distributed grass tufts hamper undulatory locomotion for this species. For the entire period until the veld has recovered sufficiently, these lizards are confronted with increased exposure, temperature fluctuations and altering insect abundance, especially grass-eating invertebrates (Warren *et al.* 1987; Mushinsky 1992, Cavitt 2000). This nutritional constraint consequently increases the risk of starvation for *C. anguina*, which ultimately may influence the reproductive cycle of individual females due to insufficient energy reserves. I propose that females surviving a fire are confronted with different sets of environmental factors after the fire and that these factors may then influence the females differently, altering the timing of reproductive events of some of them.

The second possibility is that reproduction in *C. anguina* is aseasonal. This means that even in the absence of veld fires, the reproductive events of females will never be synchronized, because the reproductive pattern is genetically based. This hypothesis can be tested by comparing the timing of reproductive events of *C. anguina* females from an area that has not burned for a long period of time, with that of females from an area subjected to a high fire frequency. If a significant difference between the reproductive patterns of the females from these two localities exists, it can be assumed that reproductive events are easily disrupted by environmental changes brought about by veld fires.

Aseasonal reproduction exhibited by this species, cannot be attributed to the fact that the specimens were collected from a wide geographical area with diverse local climatic conditions. The reproductive cycles of females collected from only the Western Cape, having a clear winter rainfall pattern with low temperatures (Figure 4.1), were also not synchronized.

4.4.2 Male reproductive cycle

The significant seasonal variation that existed in both testes volume and seminiferous tubule diameter, as well as the histological examination, indicated that *Chamaesaura anguina* males follow a annual spermatogenic cycle described as post-nuptial. This type of cycle is characterized by summer/autumn spermatogenesis and sperm storage throughout winter (Guillette & Mendez-de la Cruz 1993). *Chamaesaura anguina* males differ from other cordylids that display a post-nuptial cycle, in that spermiogenesis already starts in spring. Although I do not have adequate data to be confident that maximum spermatogenesis in *C. anguina* is reached during autumn, there definitely is testicular regression during winter. Reproductive asynchrony between males and females, which is normally associated with a post-nuptial testicular cycle, suggests that the sexes respond to different environmental cues or to the same cues in a different fashion (Guillette & Mendez-de la Cruz 1993). Because sufficient energy reserves are not as essential for the maintenance of the testicular cycle as it is for maintaining the ovarian cycle, the male reproductive cycle is probably not disrupted by environmental events like veld fires. The post-nuptial cycle in *C. anguina* is, according to the cordylid phylogeny proposed by Frost *et al.* (2000), a plesiomorphic character, and cannot be considered an adaptation related directly or indirectly to fire. *Cordylus giganteus* (Van Wyk 1995), *Pseudocordylus melanotus* (Flemming 1993b), and *P. microlepidotus* (Sachse, unpublished data) are other representatives of the Cordylidae studied to date that also exhibit a post-nuptial spermatogenic cycle. This is in contrast to the pre-nuptial cycle displayed in other cordylids studied to date, *Cordylus polyzonus* (Van Wyk 1990; Flemming 1993a), *C. cordylus* (Jacobs, unpublished data); *Platysaurus minor* and *P. capensis* (Van Wyk & Mouton 1996). There are no obvious common

denominators among cordylids following a post-nuptial cycle that can give any indication of the functional and evolutionary significance of a post-nuptial cycle.

4.4.3 Sexual dimorphism and clutch size

Female-biased dimorphism in SVL recorded for *Chamaesaura anguina* corresponds with the general pattern recorded for cordylids, in which terrestrial forms display female-biased dimorphism, and rupicolous forms male-biased dimorphism (Van Wyk & Mouton 1998; Mouton *et al.* 1999). The SDI and SDImax calculated for *C. anguina* is more than one and a half times higher than the SDI and SDImax calculated for *Cordylus macropholis* (Mouton *et al.* 2000) and *C. giganteus* (Van Wyk 1992), which means a greater difference between the SVL of males and females.

Sexual dimorphism can have a genetic basis, resulting from sexual selection or natural selection (Vitt & Cooper 1985), or be of epigenetic origin resulting from a broad array of local environmental influences (Shine 1990; Mouton *et al.* 2000). Based on Darwin's 'fecundity advantage' hypothesis that natural selection should favour larger female body sizes to allow them to produce more offspring, I conclude that the longer SVL of *C. anguina* females is the result of natural selection. The significant positive correlation that exists between SVL and clutch size confirms this conclusion. Unlike *C. anguina* lizards, clutch size in most viviparous members of the Cordylidae is small and does not increase with an increase in female body size (Van Wyk & Mouton 1998). Clutch sizes of 3 - 17 in *C. anguina* (Boycott 1990; Branch 1998; personal observation), are much bigger than the clutch sizes of 1 - 5 in other cordylids (Branch 1998). Higher fecundity may in itself be an adaptive survival strategy for this lizard species sensitive to fire in an unpredictable fire prone environment. This is advantagous for the species, because successful recruitment after a fire is facilitated by high fecundity.

Gravid females of many viviparous reptiles experience higher mortality owing to reduced locomotor performance (Charland & Gregory 1995). The burden of carrying developing embryos is assumed to impose a cost for these reptiles. During collection, the grass lizards that did not flee, or that fled slowly from the collector, were all gravid females. The male and non-gravid female grass lizards all fled with great speed and agility, making it an almost impossible task to catch them. In the case of a fire, the gravid *C. anguina* females would most likely be more susceptible than other individuals of the species. Obviously, fecundity in *C. anguina* is a trade off between recruitment potential and locomotor impairment.

Combined with fecundity selection, is the reduction of body diameter. This is induced by this species' terrestrial lifestyle, resulting in female-biased SSD in *C. anguina*. Elongate lizards with reduced limbs usually occur in densely vegetated microhabitats (Gans 1975). In such cases, selection prefers a small body diameter, allowing the lizard to pass through narrow gaps and crevices (Gans 1975). The reduction in body diameter, which results in the reduction in the relative amount of abdominal volume in females used to carry embryos or eggs (see Griffith 1994), can be compensated for by elongation of the axilla-groin section (Bauwens *et al.* 1997; Mouton *et al.* 2000).

Female-biased SSD has, to date, been recorded in three other cordylid species, of which two are terrestrial and the other one rupicolous. Female-biased dimorphism in *C. macropholis* (Mouton *et al.* 2000) can be ascribed to the combined effects of a reduction of body diameter induced by its terrestrial lifestyle, and fecundity selection, while it is not clear whether female-plus dimorphism in *C. giganteus* (Van Wyk 1992) is due to differences in abdomen length. The sample of *Pseudocordylus capensis* lizards used in the study of Van Wyk & Mouton (1998) were collected from various

localities, and the observed female-biased dimorphism may be an artifact of geographical size variation and sample size.

4.4.4 Summary and conclusions

The reproductive pattern observed in *Chamaesaura anguina* females does not conform to the regular cordylid autumn/winter vitellogenic pattern. Female reproductive events are poorly synchronized, and this may be an adaptive survival strategy to a fire-prone environment or simply a phenotypic response by individual females to different environmental conditions after a fire. The significant seasonal variation that existed in testes volume and seminiferous tubule diameter, as well as the histological examination of the testes, indicated that *C. anguina* males follow an annual spermatogenic cycle best described as post-nuptial. This type of cycle is characterized by summer/autumn spermatogenesis, associated with sperm storage throughout winter. *Chamaesaura anguina* males differ from other cordylids following a post-nuptial cycle, in that spermiogenesis already commences in spring. The arrangement of body size classes indicates that female *C. anguina* lizards reach larger sizes than males. Female-biased dimorphism in SVL corresponds with the general pattern recorded for cordylids, in which terrestrial forms display female-biased dimorphism, and rupicolous forms male-biased dimorphism. The longer SVL of *C. anguina* females is the result of natural selection to facilitate higher fecundity. This may in itself be an adaptive survival strategy for this lizard species sensitive to fire in an unpredictable fire prone environment, because successful recruitment is facilitated by high fecundity.

REFERENCES

AVERY, R.A., MUELLER, C.F., SMITH, J.A. & BOND, D.J. 1987. The movement patterns of lacertid lizards: speed, gait and pauses in *Lacerta vivipara*. *J. Zool. Lond.* **211**: 47-63.

BAARD, E.H.W. 1997. The dynamics of two sympatric tortoise communities in a stressful environment. Proceedings of the Third H.A.A. Symposium. Pretoria, 11-15 October 1993. Herpetological Association of Africa.

BAARD, E.H.W. Weskus brande eis tot 282 000 rooipensskilpaaie. *Die Burger*, 2 September 2000, 3.

BALLINGER, R.E. 1973. Experimental evidence of the tail as a balancing organ in the lizard, *Anolis carolinensis. Herpetologica* **29**: 65 – 66.

BAMFORD, M.J. 1995. Responses of reptiles to fire and increasing time after fire in *Banksia* woodland. *CALM Science Supl.* **4**: 175-186.

BAUWENS, D., CASTILLA, A.M. & MOUTON, P. LE F.N. 1999. Field body temperatures, activity levels and opportunities for thermoregulation in an extreme microhabitat specialist, the girdled lizard, *Cordylus macropholis*. *J. Zool.* **249**: 11-18.

BAUWENS, D., CASTILLA, A.M. & VAN DAMME, R. 1990. Field body temperatures and thermoregulatory behavior of the high altitude lizard, *Lacerta bedriagae*. *J. Herpetol.* **24**: 88-91.

BISSINGER, B.E. & SIMON, C.A. 1979. Comparison of tongue extrusions in presentatives of six families of lizards. *J. Herpetol.* **13**: 133-139.

BOYCOTT, R.C. 1990. Cordylidae: *Chamaesaura anguina*, Cape grass lizard, size, reproduction and susceptibility to fire. *J. Herp. Assoc. Afr*. **37**: 49.

BRADSHAW, S.D. 1986. *Ecophysiology of Desert Reptiles*. Academic Press, Sydney.

BRANCH, B. 1998. *Field Guide to Snakes and other Reptiles of Southern Africa*, 3rd ed. Struik Publishers, Cape Town.

BRUNING, J.L. & KINTZ, B. 1977. *Computational Handbook of Statistics*, 2nd ed. Scott Foresman, Glenview.

BRUSCA, R.C. & BRUSCA, G.J. 1990. *Invertebrates*. Sinauer Associates, Sunderland.

CAVITT, J.F. 2000. Fire and a tallgrass prairie reptile community: Effects on relative abundance and seasonal activity. *J. Herpetol.* **34**: 12-20.

CHARLAND, M.B. & GREGORY, P.T. 1995. Movements and habitat use in gravid and nongravid female garter snakes (Colubridae: *Thamnophis*). *J. Zool., Lond.* **236**: 534-561.

CHENEY, N.P. 1981. Fire behaviour. In: *Fire and the Australian Biota*, (eds) Gill, A.M., Groves, R.H. & Noble, I.R. Australian Academy of Science, Canberra.

CHODROW, R.E. & TAYLOR, C.R. 1973. Energetic cost of limbless locomotion in snakes. *Fed. Proc.* **32**: 422.

CHRISTIAN, K.A. & WEAVERS, B.W. 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecol. Monogr.* **66**: 139-157.

COLLINS, S.L. & GIBSON, D.J. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. In: *Fire in North American Tallgrass Prairies*, (eds) Collins, S.L. & Wallace, L.L. Oklahhoma Univ. Press, Norman. pp. 81-98.

COOPER, W.E., JR. 1989. Absence of prey odor discrimination by iguanid and agamid lizards in applicator tests. *Copeia* **1989**: 472-478.

COOPER, W.E., JR. 1990a. Prey odor detection by teiid and lacertid lizards and the relationship of prey odor detection to foraging mode in lizard families. *Copeia* **1990**: 237-242.

COOPER, W.E., JR. 1990b. Prey odor discrimination by anguid lizards. *Herpetologica* **46**: 183-190.

COOPER, W.E., JR. 1992. Prey odor discrimination and poststrike elevation in tongue flicking by a cordylid lizard, *Gerrhosaurus nigrolineatus*. *Copeia* **1992**: 146-154.

COOPER, W.E., JR. 1994a. Multiple functions of extraoral lingual behaviour in iguanian lizards: prey capture, grooming and swallowing, but not prey detection. *Anim. Behav.* **47**: 765-775.

COOPER, W.E., JR. 1994b. Prey chemical discrimination, foraging mode and phylogeny. In: *Lizard Ecology: Historical and Experimental Perspectives*, (eds) Vitt, L.J. & Pianka, E.R. Princeton University Press, Princeton. pp. 95-116.

COOPER, W.E., JR. 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Anim. Behav.* **50**: 973-985.

COOPER, W.E., JR. 1997. Correlated evolution of prey chemical discrimination with foraging, lingual morphology and vomeronasal chemoreceptor abundance in lizards. *Behav. Ecol. Sociobiol.* **41**: 257-265.

COOPER, W.E., JR. & BURGHARDT, G.M. 1980. Vomerolfaction and vomodor. *J. Chem. Ecol.* **16**: 103-105.

COOPER, W.E., JR. & VAN WYK J.H. 1994. Absence of prey chemical discrimination by tongue-flicking in an ambush-foraging lizard having actively foraging ancestors. *Ethology* **97**: 317-328.

COOPER, W.E., JR., WHITING, M.J. & VAN WYK J.H. 1997. Foraging modes of cordyliform lizards. *S. Afr. J. Zool.* **32**: 9-13.

COWLING, R.M. & RICHARDSON, D. 1995. *Fynbos: South Africa's Unique Floral Kingdom.* Tien Wah Press, Singapore.

CRUZ, F.B., TEISAIRE, E., NIETO, L. & ROLDAN, A. 1999. Reproductive biology of *Teius teyou* in the semi-arid Chaco of Salta, Argentina. *J. Herpetol.* **33**: 420-429.

DEACON, H.J., JURY, M.R. & ELLIS, F. 1992. Selective regime and time. In: *The Ecology of Fynbos: Nutriets, Fire and Diversity*, (ed) Cowling, R. Oxford University Press, Cape Town. pp. 6-22.

DUNHAM, A.E., MILES, D.B. & RESNICK, D.N. 1988. Life history patterns in squamate reptiles. In: *Biology of the Reptilia. Ecology B: Defense and Life History*, (eds) Gans, C. & Huey, R.B. Alan Liss, New York. Vol. 16, pp. 441-522.

DUVALL, D., GUILLETTE, L. & JONES, R. 1982. Environmental control of reptilian reproductive cycles. In: *Biology of the Reptilia*, (eds) Gans, C. & Pough, H. Academic Press, New York. Vol. 13, pp. 201-231.

EDWARDS, D. 1984. Fire regimes in the biomes of South Africa. In: *Ecological Effects of Fire in South African Ecosystems*, (eds) P. de V. Booysen, P. de V. & Tainton, N.M. Springer-Verlag, Berlin. pp. 19-37.

ERWIN, W.J. & STASIAK, R.H. 1979. Vertebrate mortality during the burning of a reestablished prairie in Nebraska. *Amer. Midl. Natur.* **101**: 247-249.

FITCH, H.S. 1970. Reproductive cycles of lizards and snakes. *Misc. Publ. Univ. Kansas Mus. Nat. Hist.* **52**: 1-247.

FITCH, H.S. 1987. Reproductive cycles in tropical reptiles. *Occ. Papers Mus. Nat. Hist. Univ., Kansas* **96**: 1-53.

FLEMMING, A.F. 1993a. The female reproductive cycle of the lizard *Pseudocordylus m. melanotus* (Sauria: Cordylidae). *J. Herpetol.* **27**: 103-107.

FLEMMING, A.F. 1993b. The male reproductive cycle of the lizard *Pseudocordylus m. melanotus* (Sauria: Cordylidae). *J. Herpetol.* **27**: 473-478.

FLEMMING, A.F. & VAN WYK, J.H. 1992. The female reproductive cycle of the lizard *Cordylus p. polyzonus* (Sauria: Cordylidae) in the southwestern Cape Province, South Africa. *J. Herpetol.* **26**: 121-127.

FROST, D., JANIES, D., MOUTON, P. LE F.N., & TITUS, T. 2000. A molecular perspective on the phylogeny of the girdled lizards (Cordylidae, Squamata). *Am. Mus. Novitates* (in press).

FUENTES, E.R. & JAKSIC, F. M. 1979. Activity temperatures of eight *Liolaemus* (Iguanidae) species in central Chile. *Copeia* **1979**: 546-548.

FYFE, G. 1980. The effect of fire on lizard communities in central Australia. *Herpetofauna* **12**: 1-9.

GANS, C. 1975. Tetrapod limblessness: Evolution and functional corollaries. *Amer. Zool.* **15**: 455-467.

GARLAND, T. JR. 1993. Locomotor performance and activity metabolism of *Cnemidophorus tigris* in relation to natural behaviors. In: *Lizard Ecology: Historical and Experimental Perspectives*, (eds) Wright, J.W. & Vitt, L.J. Princeton University Press, New Jersey. pp. 163-210.

GARLAND, T. JR. & LOSOS, J.B. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: *Ecological Morphology, Integrative Organismal Biology*, (eds) Wainwright, P.C. & Reilly, S.M. University of Chicago Press, Chicago. pp. 240-302.

GIBBONS, J.W., & LOVICH, J.E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetol. Monogr.* **4**: 1-29.

GILL, A.M. 1975. Fire and the Australia flora: a review. *Australian Forestry* **38**: 4-25.

GRIFFITH, H. 1994. Body elongation and decreased reproductive output within a restricted clade of lizards (Reptilia: Scincidae). *J. Zool., Lond.* 233: 541-550.

GRIFFITHS, A.D. & CHRISTIAN, K.A. 1996. The effects of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. *Aust. J. Herpetol.* **21**: 386-398.

GUILLETTE, L.J. JR. & MENDEZ-DE LA CRUZ, F.R. 1993. The reproductive cycle of the viviparous Mexican lizard *Sceloporus torquatus*. *J. Herpetol.* **27**: 168-174.

HALPERN, M., & KUBIE, J.L. 1980. Chemical access to the vomeronasal organs of garter snakes. *Physiol. Behav.* **24**: 367-371.

HEATWOLE, H. 1976. *Reptile Ecology*. University of Queensland Press, Queensland.

HERSELMAN, Y.M. 1991. A revision of the taxonomic status of *Pseudocordylus capensis* (Sauria, Cordylidae). M.Sc. thesis. University of Stellenbosch, Stellenbosch.

HUEY, R.B. 1982. Temperature, physiology, and the ecology of reptiles. In: *Biology of the Reptilia*, (eds) Gans, C. & Pough, F.H. Academic Press, London. Vol 12, pp. 25-91.

HUEY, R.B. 1991. Physiological consequences of habit selection. *Amer. Nat.* (Suppl.) **137** : S91 – S115.

HUEY, R.B. & PIANKA, E.R. 1981. Ecological consequences of foraging mode. *Ecology* **62**: 991-999.

HULBERT, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology* **50**: 874-77.

HUMASON, G.L. 1967. *Animal Tissue Techniques*. W.H. Freeman, San Francisco.

JAMESON, E.W., JR. 1988. *Vertebrate Reproduction*. John Wiley and Sons, New York.

JOHNSON, E.A. & VAN WAGNER, C.E. 1985. The theory and use of two fire history models. *Can. J. Forest Research* **15**: 214-20.

KIESTER, A.R., GORMAN, G.C. & ARROYO, D.C. 1975. Habitat selection behavior of three species of *Anolis* lizards. *Ecology* **56**: 220-225.

LANG, M. 1991. Generic relationships within Cordyliformes (Reptilia: Squamata). *Bull. Inst. R. Sci. Nat. Belg. Biol.* **61**: 121-188.

LE MAITRE, D.C. & MIDGLEY, J.J. 1992. Plant reproductive ecology. In: *The Ecology of Fynbos: Nutriets, Fire and Diversity*, (ed) Cowling, R. Oxford University Press, Cape Town. pp. 6-22.

LICHT, P. 1967. Environmental control of the annual testicular cycle in the lizard, *Anolis carolinensis*. I. Interaction of light and temperature in the initiation of testicular recrudescence. *J. Exp. Zool.* **165**: 505-516.

LICHT, P. 1984. Seasonal cycles in reptilian reproduction. In: *Marshall's Physiology of Reproduction*, (ed) Lemming, E. Academic Press, New York. pp. 206-282.

LOSOS, J.B. & IRSCHICK, D.J. 1996. The effect of perch diameter on escape behaviour of Anolis lizards: lab predictions and field tests. *Anim. behav.* **51**: 593 – 602.

MACARTHUR, R.H. & PIANKA, E.R. 1966. On optimal use of a patchy environment. *Am. Nat.* **100**: 603-609.

MAYHEW, W.W. 1963. Reproduction in the granite spiny lizard *Sceloporus orcutti*. *Copeia* **1963**: 144-152.

MAYHEW, W.W. 1971. Reproduction in the desert lizard, *Dipsosaurus dorsalis*. *Herpetologica* **27**: 57-77.

MCLAUGHLIN, R.L. 1989. Search modes of birds and lizards: Evidence for alternative movement patterns. *Am. Nat.* **133**: 654-670.

MEANS, D.B. & CAMPBELL, H.W. 1981. Effects of prescribed burning on amphibians and reptiles. In : *Prescribed Fire and Wildlife in Southern Forests*, (ed) Woods, G.E. Forest Science Institute of Clemson University, Georgetown. pp. 89-96.

MENDEZ-DE LA CRUZ, F.R., VILLAGRAN-SANTA CRUZ, M. & ANDREWS, R.M. 1998. Evolution of viviparity in the lizard genus *Sceloporus*. *Herpetologica* **54**: 521-532.

MOERMOND, T.C. 1979. The influence of habitat structure on *Anolis* foraging behavior. *Behaviour* **70**: 147-167.

MOUTON, P. LE F.N. & FLEMMING, A.F. 1999. Morphological changes that accompanied transitions from rock-dwelling - to terrestrial lifestyles in cordylid lizards. Proceedings of 10th ordinary general meeting. Irakleio, 6 - 10 September 1999. Societas Europaea Herpetologica.

MOUTON, P. LE F.N. & HERSELMAN, Y.M. 1994. Paradoxical reproduction and body size in the rock lizard, *Agama atra atra*, in Namaqualand, South Africa. *S. Afr. J. Zool.* **29**: 199-203.

MOUTON, P. LE F.N. & VAN WYK, J.H. 1997. Adaptive radiation in cordyliform lizards: An overview. *Afr. J. Herpetol.* **46**: 78-88.

MOUTON, P. LE F.N., FLEMMING, A.F. & KANGA, E.M. 1999. Grouping behaviour, tail-biting behaviour and sexual dimorphism in the armadillo lizard (*Cordylus cataphractus*) from South Africa. *J. Zool.* **249**: 1-10.

MOUTON, P. LE F.N., FLEMMING, A.F. & NIEUWOUDT, C.J. 2000. Sexual dimorphism and sex ratio in a terrestrial girdled lizard, *Cordylus macropholis*. *J. Herpetol.* **34**: 379-386.

MOUTON, P. LE. F.N., GEERTSEMA, H. & VISAGIE, L. 1999. Foraging mode of a group-living lizard, *Cordylus cataphractus* (Cordylidae). *Afr. Zool.* **35**: 1-7.

MUSHINSKY, H.R. 1992. Natural history and abundance of southeastern five-lined skinks, *Eumeces inexpectatus*, on a periodically burned sandhill in Florida. *Herpetologica* **48**: 307-312.

NAGEL, H.G. 1973. Effect of spring prairie burning on herbivorous and non-herbivorous arthropod populations. *J. Kansas Entomol. Soc.* **46**: 485-96.

PERRY, G. 1995. The evolutionary ecology of lizard foraging; a comparative study. Ph.D. theses. University of Texas, Austin.

PERRY, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *Am. Nat.* **153**: 98-109.

PIANKA, E.R. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* **47**: 1055-1059.

PIANKA, E.R. 1973. The structure of lizard communities. *Ann. Rev. Ecol. Syst.* **4**: 53-74.

PIANKA, E.R. & PARKER, H.D. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. Copeia **1975**: 141-162.

POUGH, F.H. 1980. The advantages of ectothermy for tetrapods. *Am. Nat.* **115**: 92-112.

RICE, E.L., & PARENTI, R.L. 1978. Causes of decreases in productivity in an undisturbed tallgrass prairie. *Amer. J. Bot.* **65**: 1091-97.

SCHALL, J.J. 1977. Thermal ecology of five sympatric species of *Cnemidophorus* (Sauria: Teiidae). *Herpetologica* **33**: 261-272.

SCHOLTZ, C.H. & HOLM, E. 1985. *Insects of Southern Africa*. Butterworths, Durban.

SCHULTZE, R.E. & MCGEE, O.S. 1978. Climatic indices and classifications in relation to the biogeography of southern Africa. In: *Biogeography and Ecology of Southern Africa,* (ed) Werger, M.J.A. Dr W. Junk bv Publ., The Hague. pp.19 - 52.

SHINE, R. 1986. Evolutionary advantages of limblessness: Evidence from the pygopodid lizards. *Copeia* **1986**: 525-529.

SHINE, R. 1990. Proximate determinants of sexual differences in adult body size. *Am. Nat.* **135**: 278-283.

SKINNER, D.C. 1991. Effect of intraperitoneal melatonin injections on thermoregulation in the Transvaal girdled lizard, *Cordylus vittifer*. *J. Therm. Biol.* **16**: 179-184.

SOKAL, R.R. & ROHLF, F.J. 1981. *Biometry*, 2nd ed. W.H. Freeman, San Francisco.

SOULé, M. 1963. Aspects of thermoregulation in nine species of lizards from Baja California. *Copeia* **1963**: 107-115.

STAMPS, J.A. 1977. Social behavior and spacing patterns in lizards. In: *Biology of the Reptilia, Behaviour and Ecology,* (eds) Gans, C. & Tinkle, D.W. Academic Press, New York. pp. 265-322.

STAMPS, J.A. 1983. Sexual selection, sexual dimorphism and territoriality. In: *Lizard Ecology: Studies of a Model Organism,* (eds) Huey, R.B., Pianka, E.R. & Schoener, T.W. Harvard University Press, Cambridge. pp. 169-204.

STUART, C.L. & MEAKIN, P.R. 1983. A note on the effect of fire on a population of angulate tortoises, *Chersina angulata*. *J. Herp. Assoc. Afr.* **29**: 7-8.

VAN WILGEN, B.W. 1984. Fire climates in the southern and western Cape and their potential use in fire control and management. *S. Afr. J. Sci.* **80**: 358-62.

VAN WILGEN, B.W., BOND, J.W. & RICHARDSON, D.M. 1992. Ecosystem management. In: *The Ecology of Fynbos: Nutriets, Fire and Diversity*, (ed) Cowling, R. Oxford University Press, Cape Town. pp. 6-22.

VAN WILGEN, B.W., LE MAITRE, D.C. & KRUGER, F.J. 1985. Fire behaviour in South African fynbos (macchia) vegetation and predictions from Rothermel's fire model. *J. Applied Ecol.* **22**: 955-66.

VAN WYK, J.H. 1989. The female reproductive cycle of the lizard *Cordylus polyzonus polyzonus* (Sauria: Cordylidae) in the Orange Free State. *S. Afr. J. Zool.* **24**: 263-269.

VAN WYK, J.H. 1990. Seasonal testicular activity and morphometric variation in the femoral glands of the lizard, *Cordylus polyzonus polyzonus* (Sauria: Cordylidae). *J. Herpetol.* **24**: 405-409.

VAN WYK, J.H. 1991. Biennial reproduction in the female viviparous lizard *Cordylus giganteus*. *Amphibia-Reptilia* **12**: 329-342.

VAN WYK, J.H. 1992. Life history and physiological ecology of the lizard *Cordylus giganteus*. Unpubl. Ph.D. Thesis, University of Cape Town, Cape Town.

VAN WYK, J.H. 1994a. Seasonal variation in the energy reserves in the viviparous lizard, *Cordylus giganteus* (Sauria: Cordylidae). *Amphibia-Reptilia* **15**: 153-169.

VAN WYK, J.H. 1994b. Physiological changes during the female reproductive cycle of the viviparous lizard *Cordylus giganteus* (Sauria: Cordylidae). *Herpetologica* **50**: 480-493.

VAN WYK, J.H. 1995. The male reproductive cycle of the lizard, *Cordylus giganteus* (Sauria: Cordylidae). *J. Herpetol.* **29**: 522-535.

VAN WYK, J.H. & MOUTON, P. LE F.N. 1996. The reproductive cycles of the oviparous lizards *Platysaurus capensis* and *P. minor*: evidence supporting a viviparity-oviparity reversal in the Cordylidae. *Amphibia-Reptilia* **17**: 115-129.

VAN WYK, J.H. & MOUTON, P. LE F.N. 1998. Reproduction and sexual dimorphism in the montane viviparous lizard, *Pseudocordylus capensis* (Sauria: Cordylidae). *S. Afr. J. Zool.* **33**: 156-165.

VITT, L.J. 1983. Tail loss in lizards: the significance of foraging and predator escape modes. *Herpetologica* **39**: 151-162.

VITT, L.J. & CONGDON, J.D. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: Resolution of a paradox. *Am. Nat.* **112**: 595-608.

VITT, L.J. & COOPER, W.E. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. *Can. J. Zool.* **63**: 995-1002.

VITT, L.J. & PRICE, H.J. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* **38**: 237-255.

WAPSTRA, E. & SWAIN, R. 1996. Feeding ecology of the Tasmanian spotted skink, *Niveoscincus ocellatus* (Squamata : Scincidae). *Aust. J. Zool.* **44:** 205-13.

WARREN, S.D., SCIFRES, C.J., & TEEL, P.D. 1987. Response of grassland arthropods to burning: a review. *Agricult. Ecosys. Env.* **19**: 105-30.

WHEELER, P.E. 1986. Thermal acclimation of metabolism and preferred body temperature in lizards. *J. Therm. Biol.* **11**: 161-166.

WRIGHT, M.G. 1988. A note on the reaction of angulate tortoises to fire in fynbos. *S. Afr. J. Wildl. Res.* **18**: 131-133.